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CONTENTS OF VOL. VI, NOS. 2 & 3

		PAGE
1.	A Phytophthora Rot of Pears and Apples. By H. WORMALD, D.Sc. (Lond.), A.R.C.Sc. (With 2 Text-figures and Plate III)	89
2.	Notes on the Biology of *Necrobia ruficollis*, Fabr. [Coleoptera, Cleridae]. By HUGH SCOTT, M.A., Sc.D. (Cantab.). (With 2 Text-figures)	101
3.	On the Life-History of "Wireworms" of the Genus *Agriotes*, Esch., with some Notes on that of *Athous Haemorrhoidalis*, F. Part I. By A. W. RYMER ROBERTS, M.A. (With 5 Text-figures and Plate IV)	116
4.	On a Coenurus in the Rat. By M. TURNER, B.Sc. (With 1 Text-figure)	136
5.	Some Factors in Plant Competition. By WINIFRED E. BRENCHLEY, D.Sc. (With 10 Text-figures and Plate V)	142
6.	A Contribution to the Life-History of the Larch Chermes (*Cnaphalodes strobilobius*, Kalt.). By EDWARD R. SPEYER, F.E.S., M.A. (Oxon.), Carnegie Scholar. (With Diagram and Plates VI and VII)	171
7.	Studies in Bacteriosis. IV.—"Stripe" Disease of Tomato. By SYDNEY G. PAINE and W. F. BEWLEY. (With 5 Text-figures and Plates VIII and IX)	183
8.	Notes on the Life-History of *Ephestia kuhniella*. By RAYMOND V. WADSWORTH	203
9.	Notes. By J. C. F. FRYER	207
10.	Review	210

A PHYTOPHTHORA ROT OF PEARS AND APPLES.

BY H. WORMALD, D.Sc. (LOND.), A.R.C.Sc.

(*Mycological Department, South-Eastern Agricultural College, Wye, Kent.*)

(With 2 Text-figures and Plate III.)

THE ROT ON PEARS.

IN September, 1912, two pears affected with a soft rot were received at Wye from a garden in Hertfordshire. The sender stated that the disease started at the stalk end of the pears and caused them to fall before they reached maturity. The appearance at the surface of the affected pears was different from that produced by the rots commonly met with, in that there were present numerous glistening points which were evidently highly refractive granules, bearing a striking resemblance to hoar-frost. On microscopic examination these particles proved to be clusters of sporangia borne on short unbranched sporangiophores projecting in tufts through the ruptured epidermis, each sporangiophore bearing a terminal sporangium.

The rather coarse non-septate mycelium present in the discoloured tissues, and the type of sporangia found on the surface were typical of those of the Peronosporaceae, and as no record could be found of the occurrence of a member of this family on pears in this country further investigation was made.

Reference to foreign literature revealed the fact that a similar disease had been observed on apples and pears on the Continent, and on apples in America. The earliest record appears to be that of Osterwalder(4) who in the summer of 1904 found numerous fallen fruit under cordon apple trees in Switzerland. When these apples were placed in a moist chamber numerous oospores developed; on immersing the apples in water sporangia were also formed and Osterwalder was able to identify the fungus as *Phytophthora Cactorum* (Lebert et Cohn) Schröter = *P. omnivora* de Bary. In 1908 Marchal(3) described the same fungus as producing a rot of pears in Belgium, the disease causing the fruit to fall prematurely. Two years later a similar rot, also on pears, was

recorded by Bubák(1) as occurring in Bohemia; from his descriptions and figures there is reason for assuming that the disease he observed is identical with that of the Hertfordshire specimens. The clusters of sporangia, which he observed on the pears, he refers to as "stark lichtbrechen Körnchen, die habituell kleinen Zuckerkristallen ähnlich waren." About the same time Unamuno(12) found *Phytophthora Cactorum* associated with a disease of pears and cherries in Spain. In 1912 Osterwalder(5, 6) again refers to the occurrence of this fungus on apple trees in Switzerland, a die-back of the shoots being observed in this case.

While the outbreaks mentioned in the present article were under investigation two other references to fruit rots caused by a *Phytophthora* have appeared. Schoevers(11) in 1915 recorded a rot of pears in Holland attributed to *P. omnivora*, and in 1916 Whetzel and Rosenbaum(13) mention a *Phytophthora* rot of apples as occurring in America. The latter isolated *P. Cactorum* from the diseased fruit and were able to reproduce the disease on apples on the tree by inoculations with mycelium from pure cultures.

As the disease appeared to be of some economic interest and one on which no work had been done in this country more specimens were obtained, and these showed the same general features as those previously examined. The letter accompanying them stated that "the smaller variety is Fondante d'Automne, the larger one Doyenne du Comice; all the pears of the former one started to go at the base and fell within three days, now the latter pear has just commenced to fall in exactly the same way."

On keeping the affected pears in a closed glass vessel the sporangia were gradually replaced by sexual organs and oospores, the latter 22–30 μ in diameter, with smooth walls; the sexual organs were of the *Phytophthora Cactorum* type or genus *Nozemia* of Pethybridge(7). It was highly probable therefore that the sporangia and the oospores belonged to one and the same organism and inoculation and cultural experiments confirmed this supposition.

Inoculation Experiment 1. Three pears were wounded by making cuts through the skin, and sporangia from an infected pear were placed on the wounds; at the end of 20 days one of the pears had produced sporangia while on the other two only sexual organs were found. A pear which had been inoculated at the same time by placing sporangia in a drop of water in the hollow at the stalk end, without injury, showed no change after 20 days.

The fungus was then grown in pure cultures. No difficulty was

experienced in isolating it, for by transferring, on the point of a sterile needle, a few of the highly refractive granules from a diseased pear to agar, mycelium grew out and developed numerous oospores, no other organisms appearing. The fungus grew readily on such culture media as prune agar, celery agar, maize meal agar and French bean agar, and numerous oospores developed, but no sporangia were observed on these media; on nutrient starch jelly there was feeble growth and no reproductive bodies were found.

Inoculation Experiment 2. The *Phytophthora* was cultivated in the laboratory during the winter, and in the following summer two pears were inoculated with mycelium from a plate culture. Within seven days both pears were discoloured over an area extending 3·5 cm. from the point of inoculation; one showed many sporangia and sexual organs also, the other bore sexual organs only.

In order to prove conclusively the connection between the sporangia and the oospores the following cultural experiment was carried out. From one of the pears sporangia were taken and diffused in a little sterile distilled water and drops transferred with a platinum wire loop to the surface of prune agar in a Petri dish. Three of these drops, examined under a low power of the microscope, were found to contain but one sporangium each; these three were marked on the bottom of the dish, with a ring of ink round each, and kept under observation. Within 24 hours two of them had germinated and produced a number of germ tubes; in one case the germ tubes formed a diverging tuft at the non-papillate end of the sporangium, while in the other they were scattered and not localized to any particular part of the surface. The longest germ tube was 0·9 mm. in length. The two sporelings were transferred to other plates and within five days from the isolation of the sporangia, which under these conditions germinated as conidia, both had developed sexual organs similar to those observed on the pears, thus showing that the two types of reproductive bodies belong to the same fungus.

Inoculation Experiment 3. Two pears were inoculated by making a cut through the skin and placing in the wound mycelium from one of the sporelings. Within 10 days both pears had become infected and the fungus had developed the glistening particles characteristic of the disease on pears. The particles were most numerous towards the edge of the affected area, and again each was found to be a cluster of sporangia; no superficial sterile mycelium was present at such places. On the other hand, in the immediate neighbourhood of the point of inoculation mycelium was seen on the surface as a white felt; here the sporangia

were fewer in number and sexual organs were present. The affected internal tissues were found to be permeated with the non-septate mycelium. A small portion of a section, made with a sterilized razor through the infected flesh of one of the pears at 0·5 cm. below the surface, was placed on agar and gave rise to a culture similar, in general appearance and in the production of sexual organs, to those cultures obtained from sporangia.

Inoculation Experiment 4. On August 9, 1913, an experiment was carried out on pears growing in the open. Five were inoculated by making a wound through the skin and inserting mycelium from a pure culture growing on agar. Two pears were similarly wounded but sterile agar was placed in the wounds. A fortnight later one of the pears inoculated with mycelium was found on the ground and two others fell at a touch while under examination; the rest, including the controls, remained on the tree uninfected until ripe.

The pear found on the ground had been attacked by another fungus, for on keeping it in a damp chamber no fructifications appeared and a particle of the flesh placed on agar gave rise to growth unlike that of the *Phytophthora*. The other two infected pears, however, produced numerous sporangia on being kept for a few days in a damp chamber.

Two of the five pears inoculated with mycelium had therefore become affected with the *Phytophthora* rot.

Inoculation Experiment 5. In the following year an experiment was carried out on young pear trees growing in pots in the greenhouse. On September 10 eight pears were inoculated (four of each of the varieties Fondante d'Automne and Doyenne du Comice) with mycelium from a pure culture as in the preceding experiment, and on the opposite side of each pear a control wound (not inoculated) was made. At the end of six days five of the pears showed a blackened area 1·5 cm. in diameter round the inoculated wound and in a fortnight from the beginning of the experiment the rot had made distinct progress in all, half the surface in six of the pears being affected and about one quarter of the surface in the other two. On the control side of each no rot occurred at the wound except in one case in which a soft rot caused by a *Botrytis* made its appearance.

Under the conditions which obtained in the greenhouse no sporangia were seen at this stage, the atmosphere probably being too dry, so three of the infected pears (including the one with *Botrytis*) were cut off and placed in damp chambers; *Phytophthora* sporangia developed, on the side inoculated, in each case within a few days. Of the five remaining,

one was found on the ground on September 29, and two others, which were discoloured over the whole surface with the exception of a small green patch near the eye end, fell at a touch on the same day; the other two hung on the tree until October 15, by which time they were soft and discoloured over the whole surface, the stalks being brown and withered. Again no reproductive bodies were to be found on these pears while they remained in the greenhouse, but on being transferred to a damp chamber sporangia readily appeared within a few days.

About six weeks after the inoculations were made one of the pears was cut across and examined for the presence of mycelium in the tissues. Non-septate hyphae were found extending to the centre of the pear, invading the cavities of the core and forming a covering round the seeds; strands of mycelium were seen even within the seeds themselves. A small portion of the testa with the adhering mycelium was removed from one seed and after washing in several changes of sterilized distilled water it was transferred to agar in a test tube; a typical pure culture of the *Phytophthora* resulted, sexual organs developing within five days.

Inoculation Experiment 6. From one of the pears used in the last experiment sporangia were transferred to a little distilled water on a glass slide; after a few hours numerous zoospores were set free so drops containing motile zoospores were placed on the stalk end of two pears on a tree in the greenhouse on September 29, while the pears were still quite hard and not nearly ripe. One of the pears was found detached on October 2 although no signs of rot were evident. The second fell on October 9 and showed a discoloration extending from the stalk end for about 1 cm. down one side; the pear was placed in a damp chamber and within three days the rot had extended all round the stalk end to a distance of from 1·3 to 2·2 cm. and sporangia were present.

As the atmosphere in the greenhouse was rather dry the inoculations were made in the evening and the two pears were enclosed in transparent water-proof bags containing a little absorbent cotton wool soaked with distilled water; these precautions were adopted to prevent the rapid evaporation of the drops of water containing the zoospores.

The result suggests that the zoospores are able in certain circumstances to cause infection through the uninjured skin, particularly in a moist atmosphere. On repeating the experiment the following year on eleven pears, not enclosed in bags, negative results were obtained in all cases.

The Sporangia and their Mode of Germination. As found on the affected pears the sporangia were mostly elliptical or citriform; the

smaller ones were almost spherical, but others were elongate with a slight constriction near the middle. Their dimensions were in general 35–65μ × 22–35μ, the papillae being 4–6μ in length, but occasionally sporangia 70–80μ in length were observed.

The sporangiophores were 20–40μ in length and emerged through the epidermis in small tufts; each sporangiophore bore a single sporangium terminally. In certain coverglass cultures on films of prune agar, however, hyphae were produced which developed sporangia sympodially in the manner generally typical of the genus *Phytophthora*, series of 3, 4 and 5 sporangia respectively being formed in this way; no localized swellings such as are characteristic of the sporangiophores of *P. infestans* were seen on these sporangiferous hyphae.

The rich development of sporangia on pears afforded a good opportunity of studying their mode of germination. On agar they always germinated directly by giving rise to several germ tubes. In hanging drops of tap water they germinated in one of three ways, viz.

(1) Some produced branched germ tubes often swollen at the apex, with a tendency for the protoplasm to become aggregated into the swollen ends of the branches.

(2) Others gave rise to zoospores which were liberated into the water.

(3) In a few cases the protoplasm became rounded off to form zoospores which however did not escape into the water but germinated, by developing germ tubes, within the sporangium.

In distilled water the sporangia sometimes germinated by producing germ tubes directly but usually zoospores were formed, and generally numerous zoospores could readily be obtained by transferring sporangia from an infected pear to a drop of distilled water on a slide. The number of zoospores produced by a sporangium is about 30 or 40; four sporangia of which the zoospores were counted as they emerged gave rise respectively to 31, 43, 31 and 38 zoospores.

The time taken for the sporangia to become emptied was ascertained in a few instances by means of a stop-watch. Two sporangia, in which the number of zoospores was not determined, were emptied in 33 and 36 seconds respectively; in two others 31 zoospores took 31 seconds while 43 required 51 seconds. In some cases the liberation of zoospores was more irregular, thus from one sporangium 18 escaped in 20 seconds, after which 12 others, emerging more slowly, required 70 seconds, and there was still one zoospore left which remained there for some minutes. From another sporangium 25 zoospores escaped in 75 seconds; $2\frac{3}{4}$ minutes

later two others emerged, leaving 11 which were still within the sporangium after 15 minutes.

The zoospores which escape first (to about 10 in number) are difficult to count for they are expelled in an almost continuous stream and cling

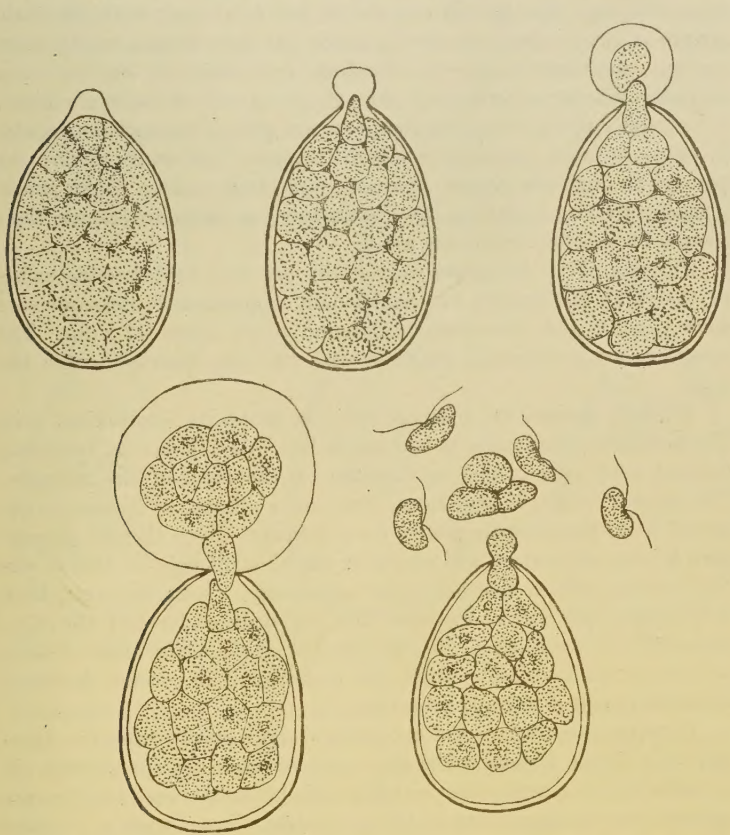

Fig. 1. Zoospores escaping from a sporangium, with the formation of a vesicle.

together, surrounded by a vesicle, just outside the mouth of the sporangium, for about a second before suddenly dispersing (Fig. 1). The vesicle is derived from the hyaline plug forming the papilla; this is pushed out as a spherical transparent body which rapidly increases in size as the zoospores rush in. When its diameter is about equal to the

length of the sporangium the vesicle suddenly becomes ruptured and disappears from view, the enclosed zoospores dispersing immediately. The rest of the zoospores come out singly in rapid succession and have to squeeze their way through the opening, becoming hour-glass shaped when half-way through. If one should fail to get out with the main stream it swims about frantically inside the now almost empty sporangium; one that was so left behind escaped eventually but took two or three minutes to force itself through the mouth of the sporangium. On reaching the exterior the zoospores are at first somewhat irregular in shape for they appear to undergo temporary deformity during the passage through the narrow aperture, and often make a slight pause, just outside the mouth of the sporangium, in order to resume their normal form before swimming away.

The size of the zoospores was usually not easy to determine owing to the rapid movements but occasionally approximate measurements were possible and the dimensions found to be about $12 \times 9\mu$. The zoospores are pyriform to reniform with two cilia inserted within the sinus.

When in motion the zoospore revolves round its longitudinal axis. The posterior cilium projects backwards like a flexible bristle, becoming inclined with each change of direction of the body of the zoospore. The anterior cilium is very rarely seen but a glimpse of it may be obtained when the zoospore pauses for a moment. Even then its appearance is only momentary and at first it was thought possible that it was the posterior cilium brought round anteriorily. Later, however, both were occasionally seen at the same time, one directed forward, the other backward. It would seem that the anterior cilium is the organ of locomotion for its invisibility when the organism is in motion doubtless indicates that it is in rapid vibration.

In those cases where the zoospores emerge slowly from the sporangium cilia can be seen while they are still inside the sporangium. It is probably the anterior cilia which are visible in this case for they are pointed towards the mouth of the sporangium; again when a zoospore is about half-way through the aperture its anterior cilium may again be seen turned over to one side, then as the zoospore becomes free the other cilium is seen trailing behind through the opening (Fig. 2).

Sometimes a zoospore was seen having a posterior attenuated "tail" of protoplasm. On one occasion two zoospores were found attached to each other by a protoplasmic strand; in such a case co-ordinated movement seemed to be absent for they swayed from side to side without

making any definite directive movement. In another instance two zoospores appeared to be attached by their cilia for a delicate fibril was seen to be connecting them; by their frantic efforts this was soon broken and they disappeared in opposite directions.

Frequently fragments of protoplasm remained just outside the mouth of the sporangium after the zoospores had swum away: these became rounded off and showed no signs of movement. The zoospores after swimming about for some time lost their motility, assumed a spherical form and began to germinate, each producing a single germ tube.

The vesicle which is produced when the zoospores are liberated from a sporangium is transparent and only just visible during the short time taken in its expansion; it is produced so rapidly and is so very evanescent,

Fig. 2. A sporangium from which the zoospores emerged slowly; the orientation of the cilia was seen under those conditions.

disappearing from view while more than half the zoospores are still within the sporangium, that it may easily escape notice, and is probably of more general occurrence than is usually supposed to be the case. The observations here recorded were made in the summer of 1913. In the same year Dastur (2) recorded and figured the vesicle for *Phytophthora parasitica*; Rosenbaum (10) in 1917 recorded having observed it in *P. Cactorum*, *P. Arecae* and *P. parasitica* and quite recently Pethybridge and Lafferty (8) have observed it in *P. cryptogea*. On the other hand Robinson (9) states that he has never observed it in the *Phytophthora* which he found associated with a Wilt Disease of Asters and assumes that the absence of the vesicle is a characteristic of the genus distinguishing it from *Pythium*.

The Rot on Apples.

In the summer of 1915 two apples affected with a soft rot were received from Surrey, the diseased areas showing, where the skin was ruptured and turned back, a white "bloom" which proved to be mycelium; a few sporangia of the *Phytophthora* type were obtained from one of the apples. Later other specimens were obtained from the same source; they were all of one variety of apple, viz. Lane's Prince Albert. The majority of these again showed the white film of mycelium where the flesh was exposed. One of them had no trace of any fungus on the surface although nearly half the apple was soft and brown; the diseased tissues however contained rather coarse, guttulate, non-septate hyphae, and particles of the flesh, cut out with a sterilized razor and placed on agar developed into cultures similar to those obtained from the *Phytophthora* on pears.

The white "bloom" was seen only on those apples where the skin had become torn and had rolled back exposing the flesh underneath; this condition obtained in most of the apples examined (see Plate III, fig. 3). In those where the skin was intact the mycelium was either not apparent at the surface or it issued through the skin as small tufts of hyphae which were quite barren, neither sporangia nor sexual organs being found on them.

Sporangia occurred far less frequently on these apples than on pears infected with the disease; of the 14 affected apples examined sporangia were found on four only at the time they were received. Osterwalder(4) found that such apples could be induced to develop *Phytophthora* sporangia freely by immersion in water, so one of the apples on which no sporangia could be found was immersed in a beaker of water which was then covered with a bell-jar. Within 24 hours a white weft of mycelium had grown out into the water; on placing a little of this mycelium on a slide numerous sporangia were seen and on adding a little distilled water numerous zoospores were liberated within two hours.

In 1917 two apples showing a similar rot, no reproductive bodies being present, were received from Sussex; the tissues however were permeated with mycelium which grew out readily when particles of the flesh were placed on agar. The resulting cultures developed sexual organs similar to those found in the other cultures.

Inoculation Experiment 7. Apples and pears were inoculated simultaneously with two strains of the fungus, one isolated from an apple, the other from a pear. The two strains gave identical results; no spor-

angia were observed in this experiment either on the infected apples or pears, but all produced sexual organs similar to those found on the naturally infected fruit and in cultures.

The morphology of the fungus causing this rot of pears and apples, particularly with respect to the sexual organs and the sporangia, conforms to that of *Phytophthora Cactorum* as given by Rosenbaum(10) who has recently made a comparative study of the genus, and as this fungus has been identified as causing a similar rot on pears and apples on the Continent and on apples in America it is to be concluded that the disease occurring in this country is identical with that found abroad.

Control Measures.

Since the fungus continues to develop on the fallen fruit these should be collected and burnt; fruit rotting on the trees should also be removed and destroyed. These precautions would tend to keep the disease in check by eliminating centres of infection, but in general would only be practicable on a small scale, as in gardens and small orchards.

As the outbreaks hitherto reported in this country have been sporadic and localized, and as the disease appears to be serious only during very wet weather at the time the fruit is approaching maturity, experiments with a view to controlling the disease by spraying have not been attempted. From analogy with other diseases caused by members of the Peronosporaceae it is probable that Bordeaux Mixture would be an effective wash as a preventive against infection, and in fact has been recommended for this disease by Marchal(3). The formula 4 : 4 : 50, i.e. 4 lbs. copper sulphate, 4 lbs. quicklime, to 50 galls. of water, gives a Bordeaux Mixture suitable for pear trees and many varieties of apples, and should be given a trial in the event of a threatened epidemic of the *Phytophthora* rot.

SUMMARY.

In wet seasons *Phytophthora Cactorum* (Lebert et Cohn) Schröter sometimes produces a rot of apples and pears in this country, causing the fruit to fall.

The rot in pears is characterized by a dark brown discoloration of the affected tissues accompanied by the appearance, at the surface, of clusters of sporangia, seen with the naked eye as glistening particles.

In apples the discoloration is paler and sporangia are less readily

produced; frequently the skin splits and the mycelium of the fungus is seen on the exposed surface as a whitish bloom.

To keep the disease in check rotting fruit, whether on the ground or still on the tree, should be collected and destroyed.

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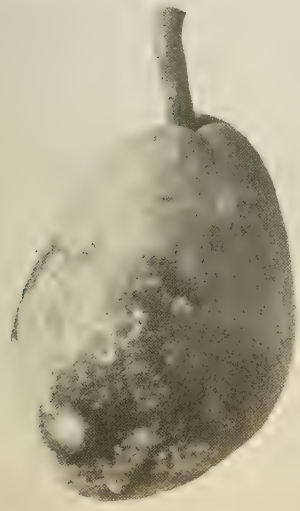
DESCRIPTION OF PLATE III

Fig. 1. A pear 6 days after inoculation with mycelium of *Phytophthora Cactorum* taken from a pure culture.

Fig. 2. The same 3 days later; by this time sporangia had developed.

Fig. 3. Apples (var. Lane's Prince Albert) affected with the Phytophthora rot.



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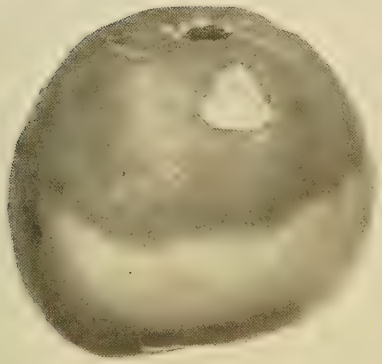

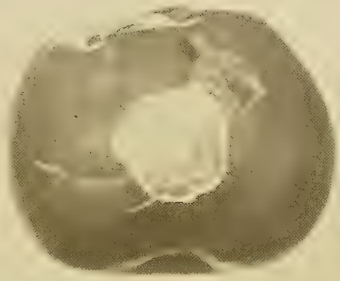

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NOTES ON THE BIOLOGY OF *NECROBIA RUFICOLLIS*, FABR. [COLEOPTERA, CLERIDAE.]

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(With 2 Text-figures.)

So much has been written about the subject of this paper that an apology for bringing the matter up again seems necessary. I had, however, opportunity to observe the insect in numbers, and can place on record some observations which are not mere repetition of any hitherto published. During 1917 and 1918, being attached as entomologist to the Hygiene Department, Royal Army Medical College, I worked in the entomological laboratory of the Imperial College of Science, South Kensington, and the observations herein recorded were made in the intervals of routine work. A large room was given up to the breeding of *Musca domestica* for experimental purposes: it was heated by radiators and bunsen burners, and a constant succession of generations of flies was maintained summer and winter alike. This fly-culture had been started late in 1915 (long before my advent at the laboratory) and was kept going continuously till late in 1917. The maggots were fed on a mixture of brown bread, casein and banana, or, late in 1917, of bran, casein and beetroot. The ingredients were thoroughly pounded and mixed, and moistened masses of the mixture were placed in large shallow vessels. The food was surrounded by sawdust in which the full-fed maggots could pupate. As fresh food was added, the lower part of the vessels became full of a mass of débris of old food, sawdust, and countless empty puparia from which flies had emerged. It was in this dark-coloured detritus that the *Necrobia*-larvae lived. They kept below the surface and were not seen unless the débris was turned over. Other denizens of this débris were one or more kinds of *Dermestes* and the moth *Tinea pallescentella*, Stainton. A bug, *Lyctocoris campestris*, Fabr. (= *domesticus*, D. and S.: Anthocoridae), was also present, though only very few of this were found. Occasionally *Fannia*, *Muscina stabulans*, *Drosophila* sp., and a minute Borborid fly[1] also bred in the dishes. Other

[1] *Limosina minutissima*, Zett. (determined by Mr J. E. Collin).

particulars and photographs of this "fly room" are given by Miss Olive C. Lodge, *Bull. Ent. Res.* IX, p. 142 and pl. VIII–XI (September, 1918).

Necrobia ruficollis was very abundant at the time of my arrival (February, 1917) and onwards. At the beginning of November, 1917, an end was put to the fly-culture, and the room was cleaned and left empty till December 12th, 1917, when a new culture was started. The *Necrobia*, however, survived these weeks of cold and absence of food, and became plentiful again in the new culture. This second culture died out in April, 1918, when for three weeks of very cold weather the room was left without heat and empty of food. The *Necrobia* scarcely survived, for though a third culture of flies was commenced in May, 1918, the beetle was not in evidence again throughout the year, excepting for one small adult seen on June 4th, 1918.

Temperature. When the heating appliances were in use, the temperature still varied somewhat with season and weather, but was generally between 70° and 80° F. (about 21° and 27° C.). The extremes which I recorded were 64° and 89° F. (about 18° and 32° C.). On some very cold nights the temperature may have fallen even lower. But the *Necrobia* was always active and at these temperatures seemed to continue breeding without intermission, regardless of the season.

Heeger (8) states that in autumn, at 9°–10° (between 48° and 50° F.) the larvae seek sheltered places for wintering, and the adults cease pairing; while at 7°–8° (between 44° and 46° F.) the adults also seek their places for hibernation[1]: and that larvae and adults awake from their winter's sleep at 8°–10°, but only commence pairing, which usually takes place in the middle of the day, when this part of the day has become decidedly warmer.

Food of the larvae. Are the larvae predaceous on maggots, etc., which live in company with them, or do they eat only dead organic matter, or resort to both kinds of diet? As far as my experience went, they could only with great difficulty be induced to kill and eat fly-maggots. This is further discussed below, after a brief review of the conclusions of earlier writers, and of the behaviour of allied species.

Heeger apparently considered them entirely saprophagous, stating ((8) p. 976) that they "suchen weiche Fetttheile, von welchen sie sich auch bis zur Verpuppung nähren." Gallois and Perris, on the other hand,

[1] Kemner (13) considers that the allied *Necrobia violacea* hibernates as an imago. In another allied species, *Necrobia rufipes*, Howard ((11) p. 106) quotes Riley ((21) p. 96) to the effect that at St Louis there are several generations annually but that the winter is invariably passed in the larval state.

thought that they are predaceous. Gallois, who observed them in great numbers in a bone store in company with *Lucilia*-larvae, remarked that when the *Necrobia*-larvae were abundant the *Lucilia*-larvae were scarce, and vice versa, and Perris ((19) p. 50) quotes him as writing in a letter "cet insecte me paraît être exclusivement carnassier...à l'état de larve, et saprophage...à l'état parfait," while Perris himself came to the same conclusion ((19) p. 51).

Taschenberg ((25) p. 16) thinks that the larvae of *N. ruficollis* have gradually given up the predaceous habit (the general habit of the Cleridae) and adopted saprophagous habits, but that sometimes they return to their primitive ways, killing and devouring fly-larvae. Cholodkovsky (1) appears to be much of the same opinion. This probably is a correct view of the case, and the observations recorded below tally with it.

The most usual habitat of *Necrobia* seems to be among bones, carrion, dried meat, skins, etc. Many writers have stated this, Curtis especially (3) emphasising that *Necrobia* differs in this respect from all the rest of the Cleridae, including *Corynetes*: all of them undergoing their metamorphoses in wood. *Necrobia* has been found more than once among insects discovered in Egyptian mummies (5, 27). It has occurred as a human parasite, a curious and probably quite abnormal case being recorded by Houlbert (9); a small larva, alive and active, was removed from a cyst in the eye of a girl of 14 years, in France. Maxwell-Lefroy (17) states that *N. ruficollis* is known to be destructive to the dry cured fish prepared in Sylhet. Kemner ((13) p. 201) found the larvae of *N. violacea* on carrion, and thinks they are probably predaceous on other larvae. Le Conte (15) in 1848 recorded this same species as covering the ground under any small piece of animal matter in the "barren regions adjoining the Rocky Mountains." Houlbert and Bétis (10) record observations to the effect that *N. violacea* and *N. ruficollis* complete the destruction of carcases commenced by Silphids and *Dermestes*. Howard (11), describing the habits of *Necrobia rufipes*, the "red-legged ham beetle," mentions no kind of larval diet except dried animal matter. I recently found a number of larvae of *N. rufipes*, in various stages of growth, on the top surface of the contents of cases of dried egg, imported from the Far East: several other species of beetles and their larvae were present[1].

[1] Since the above was written, I have seen several references to *N. rufipes* in *Rev. Appl. Ent.*, Ser. A, VI, 1918. On pp. 128 and 539 are records of its being found (in Zanzibar and Ceylon respectively) in the larval and adult states in stored copra, to which it is said to do serious damage. On the other hand, on p. 68 is an allusion to it as breeding (in the Seychelles) everywhere in salt fish, and in this case its presence in copra was regarded as accidental, due to storage of the copra and fish in the same room.

The mode of life of *Corynetes coeruleus* is distinct from that of *Necrobia*. As already mentioned, it has the normal wood-frequenting habits of the Cleridae, and the fact that it preys on Anobiids has been recorded by a number of writers (see Curtis(3) and remarks thereon by Westwood(27): also Perris(19, 20), Sharp(22), Houlbert and Bétis(10), Kemner(13), Moll(18)). These all refer to *C. coeruleus*, de Geer, or *C. ruficornis*, Sturm, which is a synonym thereof according to Schenkling (Col. Cat., Cleridae, 1910).

I tried to get actual proof that the larvae of *Necrobia ruficollis* kill fly-maggots, by isolating them, singly or in twos and threes, in small lightly-covered vessels containing a little sawdust in which the larvae could hide, and placing with them eggs or maggots of various ages of *Musca domestica*, or puparia (either sound or pierced with a needle so that the juices exuded) of *Musca* or of blowflies. The vessels were kept in the dark, as the *Necrobia*-larvae shun light. But, though no other food was provided, in none of my many experiments would the *Necrobia*-larvae attack and eat living eggs, maggots, or puparia of flies: they seemed to prefer to starve, and in some cases actually died, though whether primarily from starvation or desiccation is uncertain. But at a later date it fell to Mr R. E. Tooke, who was then working at the Imperial College, to watch some larvae, which he had isolated, in the act of killing and devouring fly-maggots: this is referred to more fully below.

As a result of these isolation experiments it appeared that: (i) the larvae probably eat the exuviae, etc., out of empty puparia from which flies have emerged; (ii) they sometimes ate their way into unbroken puparia containing fly-nymphs; (iii) they ate the soft parts of dead adult flies; (iv) they were attracted to mouldy cheese; (v) in some cases they killed, and ate the soft parts out of, fly-maggots; (vi) there was no actual proof of cannibalism, though it may have occurred in some cases where several larvae were together.

Headings (ii), (iii) and (v) are worth discussing more fully.

(ii) *Boring into intact puparia.* Perris ((19) p. 51) records finding a few puparia quite intact except for a little round hole through which the *Necrobia*-larva had entered prior to pupation within the puparium. Gallois(7) found in a sand-heap puparia of *Lucilia* which had been broken into at the head end by larvae of *Necrobia ruficollis* desirous of pupating: this caused the *Lucilia*, if fully developed, to try and break its way backwards out of its puparium at the hind end (in which effort it generally died), or, if in a less advanced stage, the *Lucilia*-nymph was crushed

against its puparium and killed by the invading *Necrobia*-larva. Gallois, however, says nothing about the *Necrobia*-larva actually *eating* the nymph of the fly. Taschenberg(25) apparently made no observation of the *Necrobia* eating into intact puparia.

On 11. iv. 1917 I placed four partly grown *Necrobia*-larvae in a vessel with a number of sound puparia of *Musca domestica* and no other food; I failed to examine them again till 2. v. 1917, by which time two of the *Necrobia* had pupated and the other two had disappeared, but five puparia had been broken into, one in two places, and cleaned out.

In the two following cases the *Necrobia*-larva was watched in the act of boring its way into an intact puparium of *Musca domestica*. My attention was drawn to one of them by Mr Ll. Lloyd, who discovered the larva in the act. In one of these cases the contained nymph may have been dead, though the puparium was intact. The first of these two *Necrobia*-larvae looked about two-thirds grown, and was found—not in one of the small vessels, but in a big vessel containing a mass of fly-maggots, food, and débris—entering the puparium (which was a small one) through a small hole on the left side of the 2nd and 3rd segments, dorso-lateral in position. Being disturbed, the larva backed out of the hole, but soon started in again, and got its whole body inside, the terminal segment and brown chitinous hooks disappearing after a few moments. During the next two hours it could be seen through the hole, moving about inside. For the next 3 days it remained in the puparium, the hole being blocked by a projecting mass of pellets of moist brown frass. When next looked at, 6 days later, the larva had come out again, having about doubled the size of the hole by eating away the substance of the puparium irregularly towards the anterior end. The puparium was absolutely cleaned out, no trace of nymphal substance being left in it. The *Necrobia*-larva was found dead a fortnight later, having refused several other kinds of food. The second larva was found (21. ii. 1917) entering a larger puparium by a hole much further back, in the 4th and 5th segments. At intervals up to 2. iii it could be seen moving about inside, the hole not being blocked; on 15. iii the hole was found blocked, and by 17. iii it was covered with the screen of hardened white secretion made by the *Necrobia* before pupation.

(iii) *Eating dead adult flies.* Several houseflies emerged from puparia in the small vessels with the *Necrobia*-larvae, and died in the vessels. Their remains were found with the soft parts of thorax and abdomen eaten out, and heads, wings and legs scattered about. [Adult *Necrobia* also ate dead flies; see below.]

(v) *Killing and eating fly-maggots.* As stated above, in none of my experiments in 1917 could the *Necrobia*-larvae be induced to attack living maggots of any age. But early in 1918 Mr R. E. Tooke watched them in the act. His observations may be recorded in his own words:

"Several larvae were placed in a receptacle containing sawdust and were left for about 24 hours without food. Two fly-larvae were then placed in the receptacle. For some time, although the *Necrobia*-larvae frequently came into contact with the fly-larvae they did nothing more than open their mandibles, more as a defensive than an offensive action. It was not until one of the fly-larvae crawled over a *Necrobia*-larva, that there was any definite attempt on the part of the latter to seize the fly-larva. Even then it seemed to be an act of defence rather than of aggression. In the resulting struggle the *Necrobia*-larva hung on tenaciously; eventually the skin of the fly-larva was ruptured and it became quiescent, and the *Necrobia*-larva commenced eating it. The soft parts were eaten out leaving the empty skin. The other larvae of the beetle also took part in eating the dead maggot, even though the second maggot was still actively moving about the vessel. This maggot was ultimately killed and eaten in the same way as was the first. Live maggots placed with other *Necrobia*-larvae were also killed and eaten. *Necrobia*-larvae were often seen to attempt to seize mites, but seemingly without success."

Pupation. Heeger(8) speaks of the "unverhüllte Verwandlung zur Puppe." In one experiment, certainly, two of my larvae did pupate fully exposed, lying on their backs, on the sawdust in a small vessel: but these had probably been subjected to unfavourable conditions, having refused several kinds of food offered to them. Normally the larvae either make a cell and line it with a hardened, opaque, white secretion, or make use of some existing cavity—notably the interior of a fly-puparium—screening all openings over with the white secretion.

The very frequent use of empty puparia of flies has been discussed by several writers (Perris, Gallois, Taschenberg, Kemner [p. 200]). I found this to be quite the favourite place for pupation, puparia of *Calliphora*, *Phormia coerulea*, and *Musca domestica* all being used. In the case observed by Gallois the puparia were those of *Lucilia*, while in that recorded by Taschenberg the fly is said to have been *Calliphora azurea*, Fallen[1]. The end of the puparium where the fly has emerged is

[1] *Protocalliphora* (or *Avihospita*) *azurea* (Fallen) is a rather scarce fly, the larvae of which have been found infesting nestling birds. Probably what is really meant is *Phormia coerulea*, R.-D., frequently but less correctly referred to as *Protocalliphora groenlandica*, Zett., a species which often breeds in profusion in bone factories and other places where dead animal matter accumulates.

screened over with a wall of the white secretion, or in the few cases where a larva has been seen to bore into an intact puparium, its entrance-hole was covered in the same way (Perris, and *ante*, p. 105). The inner surface of the puparium itself is not lined.

In my experiments there seemed to be some preference of the larvae for the more roomy blowfly-puparia, and beetles emerging from these were on the whole larger than those which had pupated in puparia of *Musca domestica*. No puparium was ever found to contain more than one *Necrobia*.

Other places besides empty puparia are used. Kemner (p. 200) cites the observations made in the Danish Zoological Museum, where larvae of *N. ruficollis* pupated not only in empty puparia of flies, but in cast larval skins of *Dermestes*, closing them with the white secretion. Kemner also quotes Lampert (14) as recording the finding of larvae of *N. ruficollis* in cork, the larval passages being closed with secretion: Kemner thinks these larvae were probably preparing to pupate in the cork, just as did those of *Corynetes* and *Opilo* kept in captivity by him.

One of my larvae pupated in a crevice in a piece of dried banana, closing the opening with the white secretion. When nothing else was available, or even in some cases where empty puparia of *Musca* were available, the *Necrobia*-larvae readily constructed cells in sawdust. They plunged down into the sawdust provided for them in small vessels, made winding burrows, and after a few days had excavated hollows, nearly always in the angle formed by the bottom and sides of the vessel. These hollows they lined with the white secretion, which held the surrounding grains of sawdust together, thus forming a cocoon which could be removed intact. Only the part of the wall of the cell formed by the glass was left uncoated with sawdust or secretion, with the result that the larvae and pupae could be seen within their pupal cells. In these cells the larvae lie not fully extended, but slightly curved. The excavation and lining of the cell appeared to take some time. Occasionally larvae were seen in cells which they had not begun to line, and once a larva was observed in a partly lined cell, with gaps in the white coating, which were not filled in till the following day.

Certain allied species make cocoons of the same type. Howard (11) describes *Necrobia rufipes* as forming papery cocoons, after boring into the muscle of hams on the fat of which the larvae had been feeding, or into neighbouring woodwork[1]. Mangan (16) also describes and figures

[1] Compare Kemner's account of the boring of wood and cork by *Opilo domesticus* and *Corynetes*. A larva of *Dermestes* which I placed in a small bottle in 1917, bored about half an inch into the cork, and pupated in the burrow,

cocoons formed by this species in bales of cotton. Information about *N. rufipes*, with small figures of its larva, pupa, and cocoon, is also given by Riley(21) and Smith(23). Kemner records that a larva of *Necrobia violacea* made itself a hollow in the cotton-wool stopper of the tube in which it was imprisoned, used its secretion also, and pupated in the cell thus formed. Perris writes of *Corynetes coeruleus* (= *ruficornis*) lining its pupal cells with white secretion: and Kemner describes how a larva of the same species, in captivity, excavated itself a hollow in the cork of the vessel, and lined the hollow with shining white material.

Though I once watched a larva, through the side of a glass vessel, turning about in its partly lined cell, and working over the walls with its mouth, I could not see whether the secretion was being actually produced from the mouth, and have found no decisive statement in the literature as to how it is produced[1].

Heeger gives 12–14 days as the duration of the pupal stage. My somewhat incomplete data indicate about 20 days as the period from the making of the cocoon to the emergence of the adult. This was at rather lower temperatures than those mentioned on p. 102, since I kept the vessels in which the larvae pupated in a room less strongly heated than the fly-room. But the larva may not become a pupa immediately after the completion of its cell, and the adult after its transformation remains in its cell for some time (a matter of days in some cases) before emerging; this could be seen, in the sawdust-cocoons, through the glass sides of the vessels. On one occasion when a number of puparia of *Musca* occupied by *Necrobia* were broken open, immediately the adult beetles, with fully developed colouring, ran actively out. Kemner ((13) p. 199) found that the pupal stage of *Corynetes coeruleus* (in captivity) lasted about a month.

Habits of adult beetles. Besides running actively, in the warm breeding-rooms the beetles frequently flew. They did not shun light as completely as do the larvae, for, though frequently found under masses

[1] Taschenberg (*l.c.*) makes some remarks on the composition of the white secretion and cites Girard (*Traité élémentaire d'Ent.* vol 1, 1873, p. 541) to the effect that Clerid larvae pupate in cells which they line with a secretion which appears to exude ("suinter") from the body, and that they collect it by scraping the abdomen with the mandibles. How far this is correct I cannot say; it does not sound very probable. Cholodkovsky (1, 2) describes and figures two large roundish glands, opening one on either side of the anus in the adult *N. ruficollis*: can they be larval secreting glands persisting in the adult? Perris ((19) p. 51) supposed the secretion to be from the anus. Kemner ((13) p. 197) thinks that in *Opilo domesticus* it comes from the mouth, because he always found the head turned towards the lid of the pupal cell, which lid is formed by the larva out of fragments of wood cemented together by the secretion.

of fly-food, etc., they also flew, ran and fed in bright light and exposed places. They appeared to eat a variety of things including dead maggots, puparia, and dead flies; possibly also the fly-food, and mouldy cheese (which they frequented in large numbers); while they repeatedly visited a shallow dish of very weak sugar-solution. The evidence was against their *killing* fly-maggots, as the following records of observations show:

29. v. 1917. A beetle was twice seen to seize a living half-grown *Musca*-maggot, both times dropping it and finally leaving it alive; the beetle then seized a second maggot, held it a few moments, then dropped it and left it also alive.

19. iv. 1917. A number of adult *Necrobia* were seen eating dead, small, partly grown, blowfly-larvae. In one place four beetles were busy on a single maggot, and during part of the time that they were watched as many as six were there; in a second case another three or four beetles were also busy on a single dead maggot. The working of the beetles' jaws was watched, and they did not appear to tear the maggots, but somehow to extract all the soft parts and leave the flabby, empty, skins to all appearance intact. The eagerness with which the beetles crowded to these two dead maggots, though there were in the same vessel large numbers of living ones of all sizes, leads one to suppose that they do not readily kill maggots; from what cause the two dead maggots had died is not known.

4. v. 1917. Three or four beetles seen greedily eating the soft parts of a blowfly-pupa, the puparium of which was broken open in some way (not, I think, by the beetles).

On another occasion three *Necrobia* emerged from the pupal stage in a small vessel. A sound puparium of *Phormia coerulea* had been opened along the same sutures as those used by an emerging fly, and the dried, mummified remains of the fly-nymph were found lying at a little distance from the empty puparium. This case is enigmatic: the puparium had not been opened before the beetles pupated, and the fly-nymph did not look developed enough to have emerged of its own accord. Could the beetles have broken open the puparium along the normal lines of weakness, and dragged out the nymph?

1. v. 1917. An adult *Necrobia* watched eating the soft parts of the abdomen of a dead blowfly, which was lying on its back; two others near it had also had their abdomens eaten out.

29. v. 1917. Two of the beetles seen eating one dead, newly-emerged housefly: no proof as to whether they had killed it or not.

NOTES ON THE LARVA AND PUPA.

The Egg is described and figured by Heeger ((8) pl. VIII, fig. 13).

Larva (fig. 1): this is fully described and figured by Heeger; Perris also describes it ((19) p. 51), and gives outlines of the terminal hooks in lateral view and of the ocelli ((19) pl. VII, figs. 243–4). Heeger's figure shows the larva as broadening markedly behind the middle, this is more noticeable in some specimens than in others, depending partly on the degree of extension of the segments. Fig. 1 shows a larva which had died with the first three abdominal segments retracted and the others much extended. The dark and light mottlings are somewhat asymmetrical and variable, but in my material there is always a fairly well-marked mid-dorsal pale line, broadening in the middle of each segment, and continuous from the eighth (penultimate) forwards to about the third abdominal segment: in front of this it becomes broken up and irregular. Heeger's figure does not show this arrangement of markings. The ventral surface is much paler, with the dark mottlings very faint, but still discernible. Ventro-lateral regions very pale, but a marked dark patch on either side nearer the front margin of each segment.

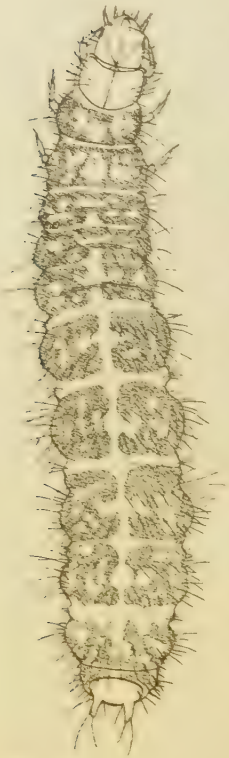

Fig. 1. × approx. 10.

The *setae* in my material are yellowish or reddish testaceous. They are more numerous than those shown in Heeger's figure, there being two bands of setae across the dorsum of each abdominal segment (at any rate in segments 1–7), and the setae of each band not always standing in a single row. In Fig. 1 they are indicated, but it is not attempted to show every one. They are more numerous in the dorso-lateral regions, where they include some very long ones. There is a small group laterally in the constriction between each two segments. Ventrally the segments appear at first sight bare, but with a high power two bands of very short setae can be seen extending across, and a group of slightly longer ones on either side.

The *terminal chitinous hooks* closely resemble those of *Necrobia*

violacea as figured by Kemner ((13) p. 206). He figures these structures in five genera of Cleridae. There is a marked difference between the pointed hooks of *Necrobia*, and their blunt truncated form in *Corynetes coeruleus*. Perris ((19) p. 52) remarks a similar difference in comparing the hooks in *N. ruficollis* with those of *Corynetes ruficornis*.

CHANGES IN SETAE AND COLOURING DURING GROWTH OF LARVA. This point does not seem to have been investigated before, but two young larvae in my material indicate that such detailed changes do occur, as might be expected. These young larvae are 4·25–4·5 mm. long (the full-grown one figured is circa 10 mm.).

The first has the head, prothorax, and tail-plate well chitinised, and of much the same colour as in the full-grown larva. The dark markings on the dorsal surface are rather sharply contrasted with the pale areas, and the arrangement of light and dark is different from that in the full-grown larva; there is no continuous pale mid-dorsal line even on the posterior segments, the dark area being continuous across the posterior part of all the segments, and across the anterior part of the meso- and meta-thorax and first two abdominal segments; the general disposition of the pale markings is to form a *transverse* rather than a longitudinal light mark across the middle of each segment. The setae are of great length in proportion to the breadth of the body, some being as long as that breadth, and these long ones occurring dorsally as well as dorso-laterally. There are short setae as well and the general arrangement appears to be in two transverse series on each segment, as in the full-grown larva.

The second small larva shows more marked differences from the full-grown larva. Its setae are differently disposed to those of the young larva just described, and it probably belongs to an earlier instar. Its head, prothoracic and tail-plates appear less strongly chitinised and are paler. The whole larva is paler, the dark markings being very faint, and not nearly as sharply contrasted with the pale, and having the appearance of faintly dusky areas of fine dots. The setae are much less numerous; very long ones occur both dorsally and dorso-laterally, but the short ones are comparatively few. The two transverse series can be discerned on each segment, but each consists of but a single row very widely spaced; each row appears to be composed, dorsally, of three very long ones, a median and two lateral, with very few, or sometimes no, shorter ones between them.

The PUPA is figured and described by Heeger. Fig. 2 is made with a drawing apparatus from one of 14 pupae which I preserved. This

example is about 5·25 mm. long: the apparent asymmetry of its head in the figure is due to its having lain in a slightly oblique position. The most striking thing about all the pupae of my material is the dark pigmentation of the abdomen, contrasted with the paleness of the other parts. Heeger does not mention this. It is indicated in my figure, but is much more noticeable on the dorsal side, where it extends all the length of the abdomen (being more concentrated laterally and towards the hind end), and some flecks of dark pigment occur also on the meso- and meta-thorax. This dark colouring is just as marked in those pupae which are less advanced, and still have the eyes quite unpigmented. It was noticed in the live pupae, and is not due to a post-mortem change. It is diffused under the cuticle, and is not due to dark intestinal contents showing through partly translucent tissues.

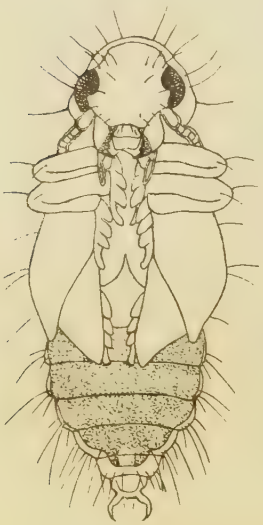

Fig. 2. × approx. 12½.

The long, fine, setae are nearly all dorsal or dorso-lateral in position. The figure indicates the disposition of such as can be seen in ventral view. They do not extend on to the ventral surface, except on the hind margins of the two abdominal segments before the last, and in the anterior of these two they only occur towards the sides. Dorsally they are numerous on the prothorax, few on meso- and meta-thorax: on each abdominal segment there is a pair on the hind margin near the middle line, and there are several in the lateral regions.

SUMMARY.

(1) *Necrobia ruficollis* bred abundantly in the "Fly Room" at the Imperial College of Science, London, in 1917–8. The larvae lived in the débris in the vessels in which houseflies were bred. This débris consisted of remains of food provided for the fly-maggots (a mixture of bread or bran, casein, and banana or beetroot), sawdust, and numbers of empty puparia.

(2) During long periods in which the room-temperature was at or above 64° F. (about 18° C.) the *Necrobia* continued breeding regardless of season.

(3) Observations made tend to confirm the view already expressed by some writers, that the larvae of this insect are usually saprophagous, but that they sometimes return to the predaceous habits characteristic of the Cleridae, and kill and devour other larvae. They were observed to eat the soft parts of dead adult flies, and to be attracted to mouldy cheese; they sometimes bore into puparia of flies (two were watched in the act); and with considerable difficulty some were induced to kill and eat fly-maggots.

(4) For pupation the larvae make use of existing cavities, and screen over all spaces with hardened, white, opaque, secretion; or they make themselves cells, and line these with the secretion. As recorded by earlier writers, a very frequent method is to enter an empty fly-puparium, and screen over the open end. But they also readily excavated and lined cells in sawdust, sometimes even when empty puparia were ready to their use. Two larvae pupated without any cell or cocoon, but this was probably a result of unfavourable conditions.

(5) The adult beetles were observed to eat dead fly-maggots and the soft parts of dead adult flies. They were attracted in numbers to mouldy cheese and to sugar-and-water. The evidence was against their killing fly-maggots.

(6) Some notes on the form of the larva and pupa are given, including observations which indicate that slight changes in the number of setae, etc., occur at the larval moults.

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The following is not intended to be an exhaustive list of every work in which allusion is made to the habits of *Necrobia*. Many of the older text-books and other writings refer briefly to the subject without making any fresh contribution to it, and the titles of these works are not all included. RUPERTSBERGER gives a number of references to articles bearing on the biology of this genus and of *Corynetes* (*Biol. d. Käfer Eur.* 1880, p. 172; *Biol. Lit. d. Käfer Eur.* 1894, p. 176): so also does SCHENKLING (*Coleopterorum Catalogus*, Part 23, Cleridae, 1910, pp. 140, 142, 143). Most or all of these are included in the list below.

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ON THE LIFE HISTORY OF "WIREWORMS" OF THE GENUS *AGRIOTES*, ESCH., WITH SOME NOTES ON THAT OF *ATHOUS HAEMORRHOIDALIS*, F.

PART I.

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(With 5 Text-figures and Plate IV.)

INTRODUCTION.

At the beginning of 1916 the necessity for increased crop production caused by war conditions, with which we had then been faced for some eighteen months, brought forward the constantly recurring "wireworm" problem more acutely than ever. Farmers were being urged to plough up more grass-land for the production of cereals and potatoes: but the reply constantly met with was that if the grass-land were ploughed up, the farmer had no security of harvesting a crop, owing to the probability that the wireworms, which were supposed to exist in great numbers in all old grass-land, would at once concentrate their attention on the crop as soon as it began to grow. The force of this reply was manifest to those who had had experience with the pests. Our knowledge of the life history, or even of its duration, was incomplete, while it was felt that none of the methods of control usually recommended could be relied upon to form a complete rejoinder to the objection of the farmer to altering his system of cultivation.

In these circumstances it was decided by the authorities at Rothamsted to make an attempt to supply some of the missing facts and work was accordingly begun in the same year.

The present paper represents the results obtained in the biology and life history of *Agriotes*, while it is hoped in the future to publish those obtained in the internal anatomy of the larva and on the research made to secure an adequate insecticide for control purposes.

Many details are still incompletely known, but as certain points of

the life history have in some measure been cleared up, it has been felt that these should be put on record without further delay.

To Dr E. J. Russell, the director of the Station, for the opportunity to carry on the work, also to Mr J. C. F. Fryer and Dr A. D. Imms, in addition to Dr Russell, for suggestions and information at many different points, my hearty thanks must be here expressed.

METHODS.

In order to obtain eggs from the parent beetles, grass plants were potted up in small (4 inch) pots and the surface of the pots enclosed by glass cylinders, the tops of which were covered by a piece of butter muslin. The beetles, when available, could be placed in the cage so formed either by removing the muslin covering the top of the glass cylinder, or by removing the whole cylinder, afterwards pressing it down a little into the soil of the pot, when replaced in position. In this manner the beetles were safely enclosed and by keeping the pots in a shady place and watering sufficiently for the needs of the plants, eggs have been obtained from *Agriotes obscurus* and *A. sputator* in 1916 and from the same two species, with the addition of *Agriotes sobrinus* and *Athous haemorrhoidalis*, in 1918. The pots, after having received their full complement of beetles, were left alone for three or four weeks to allow the beetles time to deposit their eggs without disturbance.

When it was judged that sufficient time had elapsed, the soil was carefully turned over with the point of a penknife and the eggs (if found) were laid bare. Discovery is facilitated if the soil is of a dark colour, is friable and does not contain many grains of sand, which may be mistaken for solitary eggs.

When eggs were obtained, they were taken into the laboratory and placed on damp soil in watch glasses or similar vessels for further observation. The soil being kept moist, no difficulty was experienced in hatching out the larvae. In some cases it was found necessary to pack the eggs for travel and this was done by transferring them to corked tubes containing fresh, moist, moss. Even when kept in these tubes with a bung of moss to replace the cork, for a fortnight or so, the results were satisfactory in the numbers hatched, though the ova appeared to run some risk from moulds which were inclined to spread their hyphae over the moss.

Beside the eggs which were taken from the pots for examination and observation in the laboratory, others remained and hatched in the soil of the pots. During the autumn of 1916 in view of the approaching

winter conditions and in order to give the larvae more scope for movement, the soil and grass plants from the small pots which contained larvae were bodily transferred to larger glazed earthenware pots containing more soil. These pots are the usual long pots used at Rothamsted for botanical and other pot work. They measure some 15 inches in length, 5 inches in diameter, and have a lateral bung-hole about one inch from the bottom. It was intended to sink these pots in the soil, bringing the soil-level in the pot to that of the surrounding ground. After experiment, however, great difficulty was experienced in draining the water from the pots without risk of the larvae escaping, so the pots were dug up and transferred to a lean-to shed facing North. Here they remained during the winter and the larvae, at least those of *Agriotes obscurus*, have successfully withstood the rigour of three winters under these conditions. In the summer the pots were transferred to the open and watered sufficiently to keep alive the plants of grass growing on the surface. For the first eighteen months no further supply of food was introduced, but in the spring and summer of 1918, a few slices of potato were given and have been eaten by the larvae.

In addition to the larvae bred from the egg, wild-caught larvae have been kept, in the laboratory chiefly, for observation. Owing to their predilection for a diet of their own kind, especially at times of moulting, it has been found necessary to keep each individual larva separate. Round tin "pill-boxes" or "salve boxes" have been used for this purpose, each larva being placed in a piece of turf or soil and supplied with food from time to time. It is necessary however to exercise care in giving sufficient water, for, as is well known, wire worms are excessively prone to desiccation and the soil must not therefore be allowed to become dry.

It is not pretended that these laboratory-reared larvae are reared under anything approaching natural conditions, but certain points have been elucidated by this method and wherever there is reason to doubt that observations made under such conditions would be different in the field, they can usually be checked.

I have obtained larvae from several different sources, the principal ones, beside the local ones of Harpenden, being Cambridge and Windermere.

From the latter place an almost unlimited supply has been obtained from heaps of stacked sods, originally taken from a meadow on its conversion into garden. Many pupae and newly emerged adults, principally of *Agriotes obscurus*, have also been taken from the same place.

Definition of the word "Wireworm."

Many farmers and gardeners, even yet, use the word "Wireworm" in a loose way to include millipedes and centipedes as well as the larvae of *Elateridae*. The two former must obviously be excluded, and the only question that arises in regard to the name is as to how many of the latter should be included.

In many papers on applied entomology, both in America and in this country, the term has been used to denote the larva of any Elaterid which is known to be destructive to crops. Curtis(7) himself uses it in this way; in one place (p. 153) speaking of eleven species of wireworms, though eventually (p. 189) he refers to the "true wireworms" as *Agriotes lineatus*, *A. obscurus*, *A. sputator* and *Athous haemorrhoidalis*. Westwood(25) in his *Classification* (p. 237) refers to *Agriotes lineatus* and *A. obscurus* as "the wireworm," being in some doubt whether the latter is specifically distinct from the former. He says they (i.e. the wireworms) are so called from "their cylindric form and hard texture." This definition was meant of course to apply to the two species named only, but it is equally applicable to the other species of the genus. It does not apply to an equal extent to species of other Elaterid genera which may be classed as "pests." Following Westwood therefore, the name should belong exclusively to the genus *Agriotes*.

Since, however, the word has been so generally used in recent years to denote the larva of any injurious Elaterid, it seems undesirable to define it any more closely than did Curtis, but to use it as applying primarily to the larva of the genus *Agriotes* and to that of *Athous haemorrhoidalis*, F. The larvae of other species of Elaterids may eventually also have to be included, such as those of *Athous hirtus*, Hbst. (*niger* of Brit. Cat.) and *Corymbites cupreus*, F.

The principal distinguishing characters of *Agriotes* larvae are as follow:

(i) The presence of a tooth, situated dorsally, on the inner edge of the mandible, near its apex, and

(ii) the two eye-like pits situated near the base of the 9th abdominal segment. These pits, originally supposed to be spiracles, are now usually referred to as "muscular impressions," e.g. by Ford(11) and Henriksen(15), but are believed to be sensory organs and are here referred to as "sensory pits."

Athous haemorrhoidalis, F. may be distinguished readily from all the species of *Agriotes* in the larval stage by the absence of the characters

just mentioned, by its broader and somewhat flattened appearance and by the presence on the dorsal surface of the ninth abdominal segment of a kind of impressed shield, bearing at its posterior end two pairs of prongs or cerci, which give it the appearance of possessing a bifurcated tail.

This shield is present in many other Elaterid larvae; but the orange-yellow colour of *A. haemorrhoidalis* together with the presence on the ninth abdominal segment of a single median sulcus, from which three or four transverse tributary sulci branch on either side, will serve to distinguish it from any larva with which it is likely to be confused, with the exception of *A. vittatus*—a somewhat uncommon species—and *A. longicollis*, which is rather obviously rugose above.

Relative Abundance of Species.

In Cheshire, North Staffordshire and South Lancashire, Ford found that the common "wireworm" is the larva of *Agriotes obscurus*, L. For England certainly and probably also for Wales and Scotland, the same general statement holds good. There appear to be limited districts where *A. lineatus*, L. or *A. sputator*, L. exceed it in numbers, but the predominance of either of these two latter species seems to be quite local.

Athous haemorrhoidalis, F. is a common and generally distributed beetle and to collectors frequently appears to be more common than the common species of *Agriotes*. This is however a mistake, due to the habits of the beetle itself, which flies more readily than the latter and, being found on flowers and the leaves of trees, is more readily taken with a sweeping-net. *Agriotes obscurus*, *A. lineatus* and *A. sputator* are more frequently found upon the ground or in hiding, so that their abundance as compared with *Athous haemorrhoidalis* is somewhat masked.

In order to gain some idea of the relative abundance of the species of *Agriotes* a number of well known coleopterists and economic entomologists were asked for data of adult beetles of the genus in their particular localities.

The following gentlemen have most kindly given me the benefit of their experience: Commander J. J. Walker (Oxford), Prof. G. H. Carpenter (Dublin), Prof. J. W. Carr (Nottingham), Dr W. Evans Hoyle (Cardiff), Dr R. Stewart MacDougall (Edinburgh) and Messrs G. C. Champion (Woking), F. H. Day (Carlisle), J. Davy Dean (Cardiff), J. C. F. Fryer (N. Cambs.), C. T. Gimingham (Bristol), J. N. Halbert (Dublin), B. S. Harwood (Sudbury), J. H. Keys (Plymouth), W. Mans-

bridge (Liverpool), A. V. Mitchell (Plymouth), W. E. Sharp (Crowthorne, Berks.), H. J. Thouless (Norwich), J. B. Walsh (Jarrow-on-Tyne).

The data obtained serve to confirm that of Fowler(12), from whose book the following extracts within inverted commas are taken, the remaining notes being deduced from information supplied by my correspondents:

Agriotes sputator, L. "Common and generally distributed throughout the south and midland districts of England; not so common further north." The line, north of which the species is comparatively scarce, appears to run through Norfolk, Nottingham and Cheshire.

A. obscurus, L. "Generally distributed and common throughout the kingdom."

A. lineatus, L. "Common and generally distributed throughout the greater part of England, but more local further north." Usually less common than *A. obscurus* or *A. sputator* even in the Midlands and south of England, but locally it is the dominant species, usually in low-lying positions. Such localities are the water-meadows along the Cherwell and Isis at Oxford (Walker), the banks of the river Trent in the Nottingham district (Carr); the salt marshes of the Solway (Day). In the northern Fen District, Mr J. C. F. Fryer tells me it is equally common with *A. obscurus*.

A. sordidus, Ill. "Very local and usually rare."

A. sobrinus, Kies. "Rather local;...not recorded from Scotland." This species also appears to be a southern and midland species. It is "by no means common" in Durham (Walsh) and "scarce" in Cumberland (Day), while it is not recorded in Sharp's *Coleoptera of Lancashire and Cheshire*.

A. pallidulus, Ill. "Generally distributed and common throughout the greater part of the kingdom."

Athous haemorrhoidalis, F. "Very common and generally distributed throughout the kingdom." As already mentioned this refers to the adult; the larva is less common than those of the commonest species of *Agriotes*.

So far as Scotland is concerned, Dr MacDougall reports that *Agriotes obscurus* is the commonest species; he has no record of *A. pallidulus*. In Ireland *A. obscurus* and *A. lineatus* are the only species of *Agriotes* known to occur, but both are widely distributed. Prof. Carpenter and Mr Halbert believe that *A. obscurus* is rather the commoner of the two.

GENERAL LIFE HISTORY AND HABITS.

The Imago.

When newly hatched from the pupa, the adult beetles are of a pale straw colour. From this colour they pass through a stage in which they appear of a reddish-brown colour (similar to the var. *cinnamomeus*, Buys.) and finally, as the chitin becomes hardened, assume the normal coloration of the species. The process of hardening takes some three or four days, during which the beetles remain within the earthen cell.

Most of the soil-dwelling Elaterids appear to remain in the soil during the winter, but as is pointed out in the leaflet of the Board of Agriculture(4), both *Agriotes lineatus* and *A. sputator* have been found during the winter "in tufts of grass, hedge-bottoms or refuse of dykes." In his *Coleoptera of Lancashire and Cheshire*, W. E. Sharp(22) also records *A. lineatus* as "Common in haystack refuse, etc., during winter."

So far as *A. sputator* is concerned, this habit is not universal, the beetles having been turned up in the soil during winter, though they had probably left the pupal cell previously.

In the case of *A. obscurus*, my observations in the open inclined me to the belief that this species also left its pupal cell and hibernated in the neighbouring soil. Good observers, however, have assured me that they have seen the mature beetle in the cell in winter and early spring, so that there may be a difference in habit in this respect between *A. obscurus* and the other two species named. Probably the friable nature of the soil in the locality where my observations were made is responsible for the breaking-up of the cell before the beetle was discovered.

Athous haemorrhoidalis (and it may also be mentioned *Corymbites cupreus*, F.) similarly remains in the soil during the winter, but whether within the cell or not, has not been ascertained.

In the spring the beetles emerge from their winter quarters, according to my observations, about the middle of May. Adrianov(1), observing at Kaluga in Russia, in the same latitude as Yorkshire, came to the conclusion that they had emerged earlier than May. Local climatic conditions may perhaps account for this, but during four years' observation in Hertfordshire, scarcely any *Agriotes* have been found abroad before the 15th May, although in Westmorland *A. obscurus* has been taken under stones in the first half of April.

At the end of May Adrianov found them in great numbers on the rye and wheat plants. Later they appeared on the stems and ears, very active in bright sunlight, and he considers that the pollen of rye is their favourite food. At sunset, or on cold and windy days, he found that they were hiding in the grass, under lumps of soil and so forth.

So far as *A. obscurus* and *A. sputator* (two of the species referred to by Adrianov) are concerned, my observations do not quite coincide with his. Comparatively few specimens of these two species have been taken by sweeping, either on corn or other plants. They have however been taken in great numbers on occasion under heaps of cut grass and it has been noticed that the largest numbers have been taken in dull or showery weather, as might be expected from reading Adrianov's account.

Vassiliev(23) also refers to a similar habit of hiding during the day on the part of *A. lineatus*, but says that the beetles remain in holes made by themselves, especially in hot weather—a habit which has not been observed in this country.

In contrast to the habits of the said three species, *A. sobrinus* and *A. pallidulus* and also *Athous haemorrhoidalis* are commonly taken from leaves and flowers (especially flowers of *Caucalis anthriscus*) by sweeping growing corn, clover and hedgerow plants. As to the food taken by the adults, little has been observed. *A. sobrinus* and *A. pallidulus* are evidently feeding on the nectar when found on *Caucalis* and *A. sputator* has been observed to do the same in the laboratory, though it is so seldom found on flowers in the field. Vassiliev supposed that *A. lineatus* and the other species dealt with by him (*Athous subfuscus*, *Melanotus rufipes*, *Prosternon holosericeum*) feed chiefly on the nectar of flowers, though *P. holosericeum* eats the petals of *Cytisus*.

A number of different Elaterids in America and *Limonius minutus* in Russia(19) have been recorded as damaging fruit blossom, while *Adrastus limbatus*, Brit. Cat. (= *nitidulus*, Marsh) has been known to attack Strawberries (Carpenter(5)), but so far as *Agriotes obscurus*, *A. lineatus* and *A. sputator* are concerned, little is known of the nature of their food at large beyond the statement of Adrianov.

The Egg.

The eggs of the four *Agriotes* species, *lineatus*, *obscurus*, *sputator* and *sobrinus* are laid in the soil at varying depths from a quarter of an inch down to two inches. Up to the time of going to press those of *A. lineatus* have not been procured at Rothamsted, but Adrianov obtained eggs of that species, together with *A. sputator*, in his breeding pots at depths of, approximately, $\frac{3}{4}$ to $1\frac{3}{4}$ inch, so that the site for oviposition in the four species named may be considered the same. Ova of *Athous haemorrhoidalis* have also been obtained from one of the breeding pots in a similar situation at a depth of $\frac{1}{4}$ to $\frac{1}{2}$ inch below the surface of the soil.

Adrianov found that eggs deposited too near the surface became desiccated and Graf(13) in America also found that those of *Limonius californicus*, Mannh. became desiccated when kept in a dry vial. Probably therefore the beetle descends into the soil for the purpose of obtaining a sufficiently moist nidus.

Oviposition takes place from towards the end of June to the middle of July. The ova have not been found in the open, but in the breeding pots in which the beetles have been confined from the end of May until

their death, no ova have been discovered before the early days of July. From a comparison of the time of hatching of some of the ova with that of the maximum incubation period (which is about one month) it would appear nevertheless that some of the eggs are laid in June.

Ova of both *A. obscurus* and *A. sputator* have been found in burrows excavated by the beetles in the soil, in one case the burrow appearing to be more or less horizontal, in another vertical. It is possible that this may be commonly the case but the friability of the soil when it is examined renders it uncertain whether the burrow will remain intact. The friability of the soil also makes it difficult to say whether the eggs are always laid in clusters. Certainly this is frequently the case, 52 eggs of *A. obscurus* having been taken in close proximity, but many have also been taken singly and in twos and threes and these have almost certainly not always been detached from larger clusters. In the case of *A. sobrinus*, only a few eggs have yet been taken and no clusters were

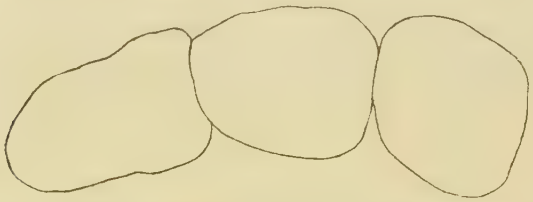

Fig. 1. Coherent ova of *Agriotes sobrinus*, Kies. Magn. × 50 approx.

found, but in the cases of each of the other two species of *Agriotes* observed, as well as in that of *Athous haemorrhoidalis*, clusters of eggs have been found.

The eggs in a cluster do not generally cohere at all fast, and no evidence has been forthcoming that they are in any real sense glued together, or to the soil in which they are laid, by any special material produced by the mother for the purpose, as is the case with some insects. Text-figure 1 is an outline drawing showing three eggs of *Agriotes sobrinus* which were coherent when dug up from the soil. One of them, which appeared to have cohered to the others in a plane at right angles to their long axes, eventually became detached under manipulation.

The actual environmental condition necessary for oviposition is a matter of the greatest practical importance and it is one which cannot at present be considered entirely solved. It seems from extrinsic evidence however to be probable that the presence of grasses, either cultivated or as weeds, is nearly, if not quite, an essential factor. Thus the typical situa-

tion in which wireworms are found in large numbers is grass-land, which has been laid down a considerable time. They may be present in arable land, but their number seems to bear a direct relationship to the state of cultivation of the land, making allowance for a ley of "seeds" or clover which will occur in the rotation.

It is concluded therefore that the eggs are laid about the roots of grasses and that such an environment is only provided by grass- or waste-land, a temporary ley (after which the wireworms found should be nearly of a size) or badly cultivated land on which couch or other grass weeds have been allowed to multiply.

The Larva.

No difficulty was experienced in hatching the young larvae, by allowing the ova to remain either on damp soil or moss. Possibly, however, there would have been trouble from desiccation, as Adrianov found, if care had not been used to supply a certain amount of moisture. The young larvae, when first hatched, at once make their way downwards into the soil and, as in the case of older larvae, appear to dislike a strong light. Except in pots where they have been known to be present, they have not been found in the soil and it is doubtful whether larvae, at least those of *lineatus*, *obscurus* or *sputator*, are ever found by farmers or gardeners in their first year of life. They are extremely small up to this age; they are pale in colour and possibly their food is not of quite the same nature as that of older larvae, so that there seems sufficient reason for their being overlooked.

Vassiliev(23) fed young larvae, up to a month or six weeks old, on rotten dung, while Adrianov found pieces of beetroot and carrot eaten to some extent and also found evidence of the larvae having eaten into the small roots of rye and wheat. In my own investigations young larvae have been kept for some weeks in tubes containing turfy soil and the gut, which is plainly visible through the cuticle, was found to be filled with a dark brown substance, evidently partially-decomposed vegetable matter. In the same way also larvae, kept in moss, have been found to have the gut filled with a green substance, the chlorophyll of the moss on which they had fed.

Some slight evidence of potato having been eaten was obtained, but it was not quite satisfactory and certainly larvae in the first instar have not been discovered boring tunnels into potato tubers in the manner of the older larvae. Tests made with growing barley at the end of the first, and during the second, instar afforded no positive evidence

of damage. Ten larvae of *A. obscurus* were enclosed in a pot with plants just above the ground. At the end of six weeks, no evidence of attack could be found and the plants appeared in no wise inferior to those in the control pot. Possibly the smaller rootlets may have been attacked, but though the length of the larvae was doubled during the experiment, the plants appeared quite healthy.

The rate of growth of the young larvae in the first instar I have found to be exceedingly slow, differing in this respect from the experience of Adrianov. His specimens of *A. lineatus*, from a length of 1·25–1·75 mm. at hatching, had obtained a length of about 4·5–5·0 mm. in eleven weeks, while *A. sputator*, from 1·0–1·5 mm., had grown in a few cases to 6 mm. or even more. As he points out, however, the total number of specimens of the latter species examined was only small and he does not regard them as typical. Other tables for the two species, reared more nearly under field conditions, show *A. lineatus* on 25th September (? 7th October by Western Calendar) to be of an average length of 4·3 mm. and of *A. sputator* 3·5 mm.

As will be seen from the data given when dealing separately with the two species, larvae of *A. obscurus* and *A. sputator* were in general found to be larger than Adrianov's at the time of hatching (2–2·75 mm. for *A. obscurus*, 1–2·5 mm. for *A. sputator*), while *A. obscurus* barely attained to the length given by Adrianov for *A. sputator* in September—October of the year of hatching by the end of the first instar (in the following June).

Larval specimens of *A. sputator* from the 1916 brood have unfortunately been few in number, but so far as the information gathered from them goes, this species appears to keep pace with *A. obscurus* in rate of growth. At the end of twelve months, either species reaches little beyond the maximum length of Adrianov's laboratory-fed specimens of only eleven weeks' growth. Possibly *A. lineatus* may be of more rapid growth than *A. obscurus*, but the few laboratory-fed *sputator* of Adrianov which reached so great a length as 6 mm. must be regarded as quite exceptional: though even the average (3·5 mm.) of the large number (44) measured by him from his outdoor cultures considerably exceeded that of either *sputator* or *obscurus* in anything approaching a similar period at Rothamsted.

At the first ecdysis, which takes place in June, the larvae of *A. obscurus* had grown but little, but during the second instar their length was about doubled. The second ecdysis occurs at the end of July and in the beginning of August, so that growth at this point is rapid. After

the second ecdysis the larva grows a little before the winter and then moults again about April or May of the following year. It is at this stage that the young larvae are generally first recognised in the field and they are then of a length of some 6·5–8·5 mm.

At the end of the second year of life, after two more ecdyses, the larvae have attained an average length of 10–11 mm., and are then very distinctly yellow. From this stage onwards observations have been made only on wild-caught larvae, but for *A. obscurus* it appears to be probable that the rate of growth is somewhat as follows:

3rd year from 11 mm. to 17–18 mm.
4th ,, ,, 18 ,, ,, 20 21 ,,
5th ,, ,, 21 ,, ,, 23–25 ,,

Such an estimate tallies with Bierkander's statement (Marsham(17)) that he had kept the larvae in confinement for five years. Ford (11) p. 101) considers this period too long, but as will be noticed from his argument on the subject, he did not take into consideration the smallness of the larvae in the first year of life—the earliest stage known to him being larvae of 7 mm. in length—nor the fact that growth in the last year is very small. The figures given above are approximate only but are taken from data of measurements of wild-caught larvae together with laboratory observations on their subsequent development.

The fact does not appear to have been generally recognised that the larvae normally moult twice in the year, in April and May and again between July and September. It appears to be true both for *A. obscurus* and *A. sputator*; also for some other species of Elaterid larvae. The summer moult is the most noticeable, since all the larvae appear to be at ecdysis at nearly the same time. At this time the larvae under natural conditions are deep in the soil, possibly as a protection from the appetites of those few which are not in the same condition and of other predaceous insects. The spring moult does not appear to take place amongst all the larvae at one time to the same extent, but there is no doubt about its occurrence. A number of cases have been noted among laboratory-fed larvae; but in addition exuviae, evidently freshly shed, have been found out-of-doors in April and larvae brought into the laboratory from outside in May have moulted within a short time afterwards. Graf(13) found the same in the case of *Limonius californicus*, an American pest of sugar-beet, but he records it in rather a tentative manner (p. 30), though evidently expecting that subsequent experience will confirm the results which he obtained in 1912.

Evidence has also been obtained that the larvae of *Athous haemorrhoidalis, Corymbites cupreus* and others which are believed to be *C. pectinicornis*, L., undergo two ecdyses in the course of the year, but this cannot yet be certainly stated.

Agriotes larvae will feed upon almost any crop and apparently upon a good many weeds, apart from grasses, which were probably their original food-plants. They are not however indifferent to the species of plant which they attack and though mustard does not appear to be absolutely immune, as was once supposed, it is probably only attacked in the absence of some more palatable plant. Charlock on the other hand appears to be favoured, larvae having been found boring into the root in cornfields, where it might be supposed their choice would be exercised otherwise. Beans usually do not suffer so much as other crops, but wireworms will on occasion attack the seed beans in the ground. Attacks in pots are difficult to induce, but in a test on a small scale, one bean out of four sown was found somewhat eaten, there having been ten wireworms in the pot. The other three beans were not affected and all four plants subsequently developed equally well.

Potatoes are often much damaged by *Agriotes* larvae and to some extent also by *Athous haemorrhoidalis*, but much of the damage done to potatoes and attributed to wireworms is in reality wrought by slugs and millipedes. *Athous haemorrhoidalis*, and also *Agriotes*, have been reported as pests of tomatoes grown in glass-houses (Carpenter(6)), the latter of course being a well-known trouble to the grower. The larvae enter the plants below the ground-level and, boring their way up the stem, kill the plants, frequently at a time when it is too late in the season to replace them. The fondness of *Agriotes* for the roots of Dock (Rumex) has been noted by Curtis ((7) p. 159) and both it and *Athous haemorrhoidalis* have been found in or about them.

It is hardly necessary to mention the propensity of *Agriotes* for attacking young growing corn, but we do not appear to suffer seriously in this country from attacks on the sown seed, though experimentally larvae have been found to hollow out corn seed in the laboratory. In the United States and other parts of America the attacks of *Agriotes* and other genera on seed is serious and they are also stated to be injurious to maize seed in Russia (Vassiliev(24)). Probably in this country the seed of cereals is sown too late in the autumn and too early in the spring to be much affected by wireworm attack before the plant develops.

Apart from the capacity of the larvae for fasting, there is no doubt that they can subsist in any ordinary soil for a very lengthy period with

no food other than humus and decaying vegetable matter. Graf(13) records an experiment made by H. M. Russell on *Limonius californicus* to test the capacity of the larvae for subsisting, as he supposed, without food. "Ordinary soil" alone was given, and, for the first thirteen months of the experiment, it was regularly watered. At the end of this time seven larvae were alive and healthy. The soil was then allowed to become dry for some two months and during this time all the larvae died except one, their bodies being removed as they died from desiccation, to prevent them from being used as a source of food by the survivors. Watering was then resumed and the one survivor continued to live until it died through an accident twenty months after the commencement of the experiment. This treatment was not of course in any sense normal to the larvae and the species dealt with of a different genus from any of our native species known to be injurious. Nevertheless the experiment throws light on the capacity of "wireworms" to withstand starvation by fallowing, *per se*, or by the use of mustard as a "starvation crop" on infested land. I have made no experiment lasting over so long a period, but from observations made in the laboratory and in pot cultures, there can be little doubt that *Agriotes* larvae would succeed in maintaining life in similar conditions for a very considerable time, if not actually for so long as *Limonius californicus*. Larvae have been kept for some months on a diet of vegetable compost during the spring and summer and in the laboratory have frequently been kept in boxes for prolonged periods with no food other than decaying roots and the humus contained in the soil. They do not thrive under such a treatment as the last named, but life is maintained and it is certain that nourishment is derived from the organic matter contained in the soil. On the other hand, provided that sufficient moisture is supplied, *Agriotes* larvae (and those of other Elaterids) are able to fast for a considerable time without apparent inconvenience. In order to test this, three larvae of different sizes were isolated in wide glass tubes containing only moistened sand which had been previously sifted and treated with acid. One larva was able to reach the cork of its tube and was found gnawing it about a week after the commencement of the experiment. At the end of one month all the larvae were found to be alive and active, having apparently suffered no ill effects from the treatment. It should be added that the experiment took place in February and March, so that there was probably no excessive reserve of fat in the bodies of the larvae such as might have been the case at the end of summer.

In the course of experiments to test the toxicity of certain substances

as insecticides, several instances of the power of the larvae to withstand starvation have also been noted. In one case, the larva was evidently affected by the insecticide, which was not of a concentration sufficient to kill it. Treated on the 21st June it still remained, three months later, in much the same condition as immediately after treatment. It was supplied with pieces of potato, but these were not eaten and eventually the larva died—whether from the effect of the insecticide or from starvation could not be ascertained.

Larval *Agriotes* can withstand immersion in water for a very long time. In glazed pots which have remained filled with rainwater for at least a few days, they have afterwards been found alive. Bierkander (17) found they could live in water for four days, but Del Guercio (8) found that death only took place after twenty to thirty days' submersion and that, as he points out, at a time (June—July) when metabolism may be considered at its height.

Graf ((13) at p. 27) notes that some of the beet fields which have suffered the most from the attacks of *Limonius californicus* are those which almost every year are quite thoroughly flooded for two or three days. It appears therefore that irrigation for any reasonable period is hardly likely to have any controlling effect.

It has been stated by Del Guercio (8) that the larvae (of *A. lineatus* and *A. obscurus*) feed during the winter between October and March, on decaying vegetable matter and it is probable that such is often the case. When grass-land has been newly ploughed, wireworms may be found, in winter, still in the sod at or quite near the surface, even in hard weather, provided that the sod remains sufficiently damp. They have also been found repeatedly in winter, when digging in the sod heaps mentioned above or on grass-land, amongst the roots of grasses growing on the surface, even during the continuance of frost and snow. Such larvae may be contracted and sluggish at the time, but appear to suffer no permanent damage and revive quickly when brought under milder conditions. At the same time that these larvae are found near the surface on grass-land, others may be found at considerable depths below. Thus, for example, in a hole dug to a depth of 31 inches in one of the sod heaps at the end of December, 1917, 14 *Agriotes* larvae were taken. Of these nearly half were taken amongst the roots of plants growing on the surface or in the first spit (9 inches) of soil, but the remainder were found lower, at depths from the surface of 14 down to 24 inches.

In the case of arable land, which has not been recently ploughed out of grass, the larvae are not found near the surface in winter, unless

perhaps in very mild weather. In a series of tests made in a field known to be infested, none were found nearer the surface than six inches, while several were found in the subsoil, which in this field was at some 10-12 inches from the surface. It is possible that larvae at such a depth might move in their burrows nearer to the surface through the influence of rain and mild weather, but it seems likely that little food, if any, would be taken between the time when they went deep into the soil and that when they returned to feed at the surface in spring. Probably therefore in many cases we have a condition of hibernation similar to that obtaining with many lepidopterous and other larvae, though in others the larvae remain in the sod at or near the surface, feeding on the roots.

As mentioned above, the larvae in the course of their movements through the soil construct burrows, so that in case of necessity they are able to retreat fairly rapidly. These burrows impress the observer when a large number of larvae are kept together in the confined space of a pot and the soil is of such a character that they remain undamaged, when it is lifted out in blocks. The burrows are then seen to honeycomb the soil, ramifying up and down and in all directions.

In the burrow the larva changes its skin, sometimes enlarging the burrow in the process to form a similar cell to that in which pupation takes place. Such cells are also frequently formed for hibernation and the larvae in a sluggish condition may be found in them in winter.

Mention must also be made of the propensity of *Agriotes* larvae for animal food alive or dead. Probably in nature little opportunity occurs to most larvae to indulge their tastes in this direction, but in captivity, as is well known, they will readily feed upon one another, even in the presence of vegetable food. Except in case of injury or at the time of ecdysis, the thick chitin of the cuticle is usually sufficient protection. At ecdysis however the larva is helpless both before and immediately after the moult takes place, so that in the case of larvae kept in a confined space the mortality is very great.

Pupal Stage.

Pupation takes place in the ground, within a cell prepared beforehand by the larva. So far as my observations extend, the pupa is placed erect in the cell, with the head uppermost. This habit has also been observed by Hyslop(16) in the case of the American species *Agriotes mancus*, Say.

The pupal instar extends over a period of about three weeks, while

pupae have been found from the latter end of July up to the middle of September.

It is often stated, for instance by Miss Ormerod (18), that the larva descends for a considerable distance beneath the surface to pupate. Reh (20) however says that it pupates close to the surface ("in geringer Tiefe") up to a depth of 10–15 cm. This also has been my experience, principally with *A. obscurus*, the following being records from my note book of two tests made by digging in the sod heaps at Windermere, each to a depth of one foot.

5. viii. 18.	2 pupae at	1″	from surface	6. viii. 18.	1 pupa at	1″	from surface
	1 pupa „	2″	„ „		2 pupae „	1–2″	„ „
	1 „ „ less	3″	„ „		1 pupa „	2″	„ „
	1 „ „	3″	„ „		1 „ „	3″	„ „
	1 „ „	4″	„ „		2 pupae „ less	4″	„ „
	1 „ „	7½″	„ „		1 pupa „	4″	„ „

Larvae pupating in pots at Rothamsted were similarly found in some cases quite near the surface and though they are found to a much greater depth than those mentioned, the habit of pupating deep in the soil, beyond the depth of a plough, is by no means universal.

Natural Enemies.

This subject has been so thoroughly dealt with in the paper by Ford (11) already quoted, that there is but little to add. In confirmation of the value of birds in reducing the number of "wireworms," reference may be made to the work of Miss Laura Florence at Aberdeen (10) especially in regard to the quantity consumed by other gulls than the black-headed gull, which has been well-known as an ally of man in this respect. Hammond's work (14) on the food of birds in the Eastern Counties of England is also of great value, bringing out, amongst other points, the fact that the skylark is of assistance in the control of these pests. Berry (3) found many wireworms in the crops of pheasants in Scotland, but Evershed and Warburton (9) appear to have found but few. Probably local and temporary conditions account for the difference.

There is no doubt that birds are one of the most important factors in the natural control of wireworms and it is probable that under conditions where such a course is possible, their numbers might be appreciably reduced if poultry, especially those of good foraging strains, were run for a time on land newly ploughed out of grass.

Wireworms do not appear to be attacked by internal parasites to any great extent. Marsham (17) records that Bierkander found six out of

thirty wireworms parasitised by an ichneumon (possibly a Proctotrupid) and Mr Fryer, as noted by Ford, has obtained Proctotrupids from *Agriotes* larvae.

In June, 1916, there emerged eleven larvae of a Proctotrupid from a larval *Athous haemorrhoidalis* taken at Windermere in the preceding April. A few days later the larvae were found to have pupated with their heads distal to the body of the host and the eyes showing dark

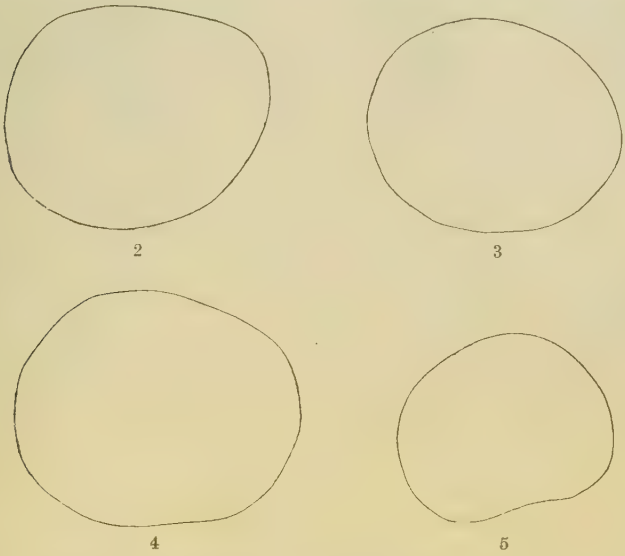

Fig. 2. *Agriotes sobrinus*, Kies.: ovum. Magn. × 75 approx.
Fig. 3. *Agriotes sputator*, L.: ovum. Magn. × 75 approx.
Fig. 4. *Agriotes obscurus*, L.: ovum. Magn. × 75 approx.
Fig. 5. *Athous haemorrhoidalis*, F.: ovum. Magn. × 75 approx.

through the creamy white integument. At this stage they resembled the figure given by Sharp(21) of pupal Proctotrupids, parasitic on an unknown beetle larva. On July 9th nine imagines emerged, one larva having been killed and one pupa having died without emerging. Five of the imagines were submitted to Mr James Waterston, of the Imperial Bureau of Entomology, who, with Dr R. C. L. Perkins, examined them and reported that all were females of a species of the genus *Phaenoserphus* (Kieff., 1908), probably *P. fuscipes* (Haliday, 1839). To these

two gentlemen my thanks must be expressed for their careful examination.

The only other case of parasitism by an insect occurred in the case of a larval *Agriotes obscurus*, probably also from Windermere, handed over to Dr Malcolm Laurie, of this station, for examination of the internal anatomy. Within the larva he found several larval parasites, which he believes are also referable to the family *Proctotrupidae*.

Wireworms are apparently parasitised by a fungus of the genus *Isaria*, as has been already stated in the Board of Agriculture leaflet (4). Critical work on the subject is necessary to be certain that the fungus is not in reality a saprophyte, though from my experience with it there is a strong presumption that it is truly parasitic.

In one of the sod heaps previously mentioned portions of larval *Agriotes* have been found on one or two occasions, consisting of a thin layer of external chitin only, the whole of the interior portions of the larvae being represented by a mass of fungus hyphae. Similar cases have occurred amongst laboratory-fed larvae obtained from the same source and the fungus has been induced to grow upon apparently healthy larvae by enclosing them in a box with an affected larva, upon portions of which they fed. Fig. 3 (Plate IV) represents the fungus growing from a specimen of *Agriotes obscurus*. The photograph was taken by Mr W. F. Bewley, to whom and to Mr W. B. Brierley I am greatly indebted for assistance and advice in dealing with this branch of our subject.

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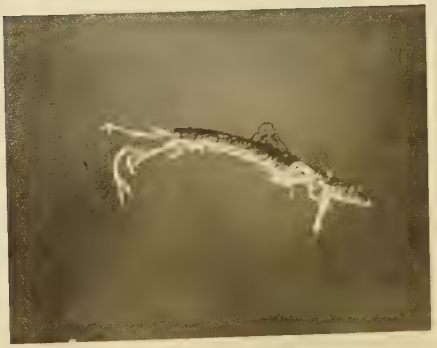

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EXPLANATION OF PLATE IV

Figs. 1 and 2. *Agriotes obscurus*, L. Larvae in 1st instar: about six weeks old. Magn. ×40 approx.

[*Photos. by Flatters & Garnett, Ltd.*

Fig. 3. Larva of *Agriotes obscurus* attacked by *Isaria* sp.

[*Photo. by W. F. Bewley.*

ON A COENURUS IN THE RAT.

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(With 1 Text-figure.)

The Rat plays so important a part in economic life and welfare of all peoples that, for many years, it has been the subject of minute and routine examinations. Because of this, its parasites are well-known and have been described in several important monographs. In 1908, Dr A. E. Shipley, Master of Christ's College, Cambridge took "Rats and their Animal Parasites" as the subject of his Presidential Address to the Association of Economic Biologists, and the same theme formed a considerable part of the Presidential Address of Dr Burton Cleland to the Royal Society of New South Wales in 1918.

One of the most common parasites of the rat is the larval tapeworm, *Cysticercus fasciolaris*, which infests the liver. Owing to the atypical appearance of this larval tapeworm it is frequently received by the Helminthological Department of the London School of Tropical Medicine for special diagnosis. With a similar object Dr W. M. Graham some years ago forwarded a collection of parasitic worms, made during a routine examination of rats at Accra, in connection with an outbreak of plague on the Gold Coast. The collection included several specimens of *Cysticercus fasciolaris*, and also a large ellipsoidal cyst which had been found in the abdomen of a rat. More recently Dr J. A. Murray, Director of the Imperial Cancer Research Laboratories, kindly sent two tapeworm cysts which came under his notice while examining mice purchased in London. Through the courtesy of Professor Leiper I was able to investigate all three cysts in detail.

The usual form of a larval tapeworm is the Cysticercus, which is a bladder-like cyst that bears on its internal surface one bud. In the definitive host this bud develops into the head of the adult worm. The cysts found in the rat and mice agree with the Cysticercus in having a vesicular shape but differ from it in having numerous buds instead of only one. For this reason the three cysts from the rat and mice belong to the group of polycephalous larval tapeworms known as "Coenurus."

No Coenurus has been recorded in either the rat or mouse before, though they have been found in other members of the group Muridae. In the Jerboa is *Coenurus polytuberculosus*, Megnin, 1880, and in the Gerbille, *Coenurus glomeratus*, Railliet et Henry, 1915.

Unfortunately the cysts from the mice are very immature, the buds having not yet developed hooks or suckers so that it is impossible to compare them with other forms of Coenurus.

Besides these from the members of the Muridae, the group Coenurus contains five more species, viz. *C. cerebralis* of sheep, *C. gaigeri* of goats, *C. serialis* of rabbits, *C. ramosus* of Macacus sinicus and *C. lemuris* of lemurs. Of these *C. cerebralis* and *C. serialis* most nearly resemble that from the rat.

Examination of the scolices of the rat Coenurus, of *C. serialis*, of *C. cerebralis* and of *C. glomeratus* has revealed the fact that there is a considerable amount of variation amongst the individual hooks. Hooks from the same scolex vary in length and shape within fairly wide limits, so that it is in some cases difficult to distinguish between two species when the material for diagnosis consists solely of a limited number of hooks.

Coenurus from the Rat.

The entire cyst is ellipsoidal in shape and measures about 2 cm. in length by 1 cm. in breadth. The cyst-wall is thin, and transparent enough to allow the buds, which cover almost the whole of the inner surface of the wall, to be clearly seen. About twenty buds project from the outer surface of the cyst. Each head, in both lateral and face view, is approximately circular in shape, with a diameter of about 650μ.

The suckers are of fairly large size. Their muscular bulbs have diameters of about 230μ. The rostellum is about 330μ in diameter and bears a double crown of from 24 to 28 hooks.

The large hooks are from 130μ to 145μ in length and the blade, handle and guard are all well developed.

The blade is moderately curved.

The handle is long and straight and very slightly tapering. Its dorsal and ventral margins are practically parallel and somewhat sinuous. A notch is sometimes present on the dorsal margin about the middle of the handle. The free end of the handle turns dorsally.

A line drawn transversely through the centre of the guard shows that the handle is considerably longer than the blade. This gives the handle a slender appearance.

The guard of the large hook is triangular in shape in lateral view, with its maximum diameter at the base. The free end of the guard is usually pointed.

The small hooks are from 90μ to 105μ in length. The blade is moderately to well curved.

The handle is quite thick and long. It is very slightly tapering at the distal extremity, is bent somewhat dorsally, and its axis meets that of the guard at an angle of from 100° to 110°.

The face view of the guards of both large and small hooks is broad, though the guard of the small hook is wider than that of the large hook. Each of these guards has tapering edges and a median groove but is not bifid.

The hooks of the *Coenurus of the rat*, of *Coenurus cerebralis*, and of *Coenurus serialis*, appear to be formed after the same type. Both the large and the small hooks are about the same size in all. The small hooks of the Coenurus of the rat and *Coenurus cerebralis* are much alike in their chief features, but that of *Coenurus serialis* differs rather markedly from these in the character of the handle. In the large hooks of all, the handle, blade and guard are well developed. In all the handle is straight in its general direction. The blades of all the large hooks are moderately curved. Nevertheless more detailed examination of my material showed that the hooks, both large and small, of each Coenurus possess some features in which they differ from the hooks of any other Coenurus, though in some cases the difference may be only one of degree.

In the material examined which consisted of one cyst from the rat, one cyst of *C. cerebralis*, and two cysts of *C. serialis*, each scolex of the Coenurus from the rat bears 24 to 28 hooks. Each of three scolices of *Coenurus cerebralis* bears 26 hooks, while each scolex of *Coenurus serialis* bears from 26 to 30 hooks. Hall, 1919, says that a scolex of *Coenurus cerebralis* bears from 22 to 32 hooks, and one of *Coenurus serialis* bears from 26 to 32. Thus the number of hooks in each scolex is about the same in the three Coenurus; viz. the Coenurus from the rat, *C. cerebralis*, and *C. serialis*.

The large hooks of the Coenurus from the rat are from 130μ to 145μ in length; those of *C. cerebralis* from 145μ to 165μ and those of *C. serialis* from 135μ to 145μ. So that here the large hooks of *C. cerebralis* are longer than those of the Coenurus of the rat and *C. serialis*. Hall gives the length of the large hooks of *C. cerebralis* as from 150μ to 170μ and the length of those of *C. serialis* as from 135μ to 175μ. In this case some of the hooks of *C. serialis* are longer than those of *C. cerebralis*.

The blade is of moderate curvature in all the large hooks. The axis of the handle in the Coenurus of the rat, in *C. cerebralis* and in *C. serialis* is straight. In all the dorsal and ventral margins of the handle are practically parallel and somewhat sinuous. The curves of these margins are large in *C. serialis*, and very slight in the Coenurus of the rat.

The handles of the large hooks of the Coenurus of the rat, of *C. cerebralis* and of *C. serialis*, all taper distally, but very slightly so in the two first and more so in the last. In all the distal end of the handle of the large hooks tends to turn dorsally. In *C. cerebralis* this dorsal bend is usually scarcely perceptible: in *C. serialis* it is more pronounced, while in the Coenurus of the rat, it is very marked in many of the hooks.

The proportion of the height of the blade to the length of the handle in the large hooks of one Coenurus is not the same as that of the hooks of another Coenurus. In all the large hooks from the Coenurus of the rat the handle is noticeably longer than the blade, which gives the handle a slender appearance. In *C. serialis* the handle may be somewhat longer than the blade though usually they are about equal. In *C. cerebralis* the blade is longer than the handle so that the handle appears strong and thick.

A notch is frequently present on the dorsal margin of the handle of the large hook of *C. cerebralis* and is often seen in some hooks of the Coenurus of the rat.

One of the chief features by which these large hooks may be distinguished is the shape in lateral view of the guards. In the hooks of the Coenurus of the rat the guard is triangular with its maximum diameter at the base and usually with a pointed distal end. The guard of *C. cerebralis* is practically cylindrical for some way out from its base and then tapers sharply to its free extremity. Its greatest diameter is usually just before the guard begins to taper.

In the majority of the large hooks of *C. serialis* the guard is almost cylindrical with a blunt rounded tip.

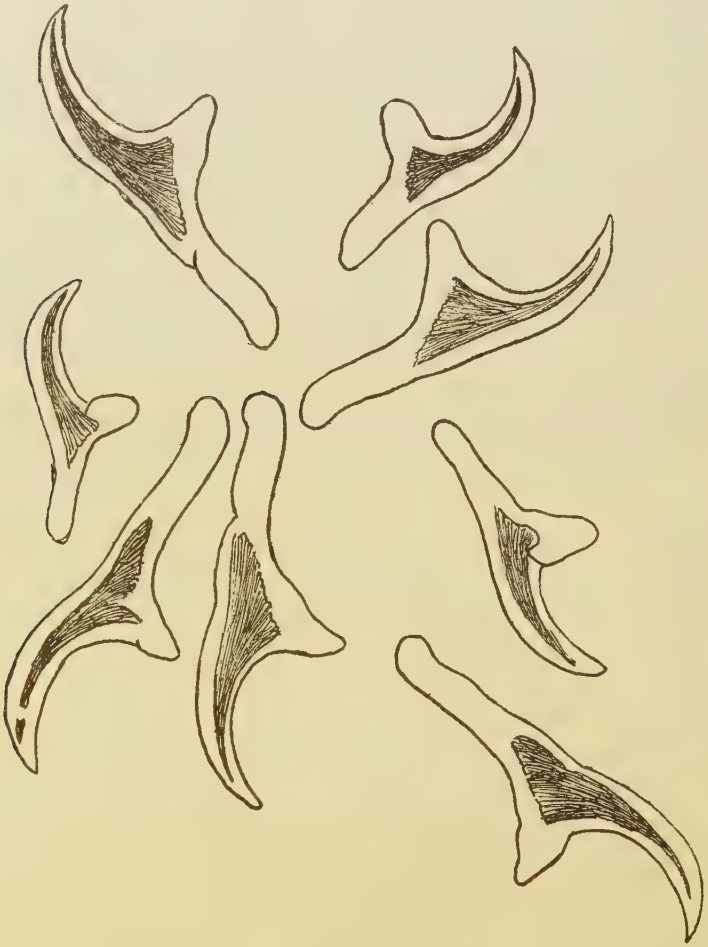
In *C. cerebralis* and *C. serialis* the core of the hook does not enter the guard but in the hooks of the Coenurus of the rat it penetrates the broad base of the guard for a short way.

The axes of the guard and the handle of the large hooks of each Coenurus meet at about 90°.

In my material the small hooks of the Coenurus from the rat are from 90μ to 105μ in length: those of *C. cerebralis* are from 95μ to 120μ (Hall gives 90μ to 130μ) and those of *C. serialis* from 90μ to 100μ (Hall gives 78μ to 120μ). So that the small hooks of *C. cerebralis* are the longest.

The curve of the blade of the small hook of each Coenurus is from moderate to strong.

The guard is well developed in all three small hooks. Their shape in



Hooks of a Coenurus from a rat.

each Coenurus is not so constant as that of the guards of large hooks. Yet the guard of the small hook of the Coenurus from the rat is usually almost cylindrical with a rounded tip. In the small hooks of *C. cerebralis* the guard is usually long and tapering, while in those of *C. serialis* it is

usually short and rounded. The face view of the guards of all the hooks of the Coenurus from the rat, of *C. cerebralis* and *C. serialis*, is broad, and in all it is wider in the small hooks than in the large.

The small hooks of the Coenurus from the rat and of *C. cerebralis* have quite long handles, which are tapering in both but those of *C. cerebralis* are more so than those of the Coenurus from the rat. The handles of the small hooks of *C. serialis* are usually short. In the small hook of the Coenurus from the rat and in *C. cerebralis* the axes of the guard and handle meet at an angle of from 100°–110°. In *C. serialis* this angle is from 130°–140°. All the handles bend somewhat dorsally, but as these figures show, that of the small hook of *C. serialis* is much more curved than those of either of the small hooks of the Coenurus of the rat or of the small hooks of *C. cerebralis*.

The differences in the hooks of the Coenurus of the rat of *C. cerebralis* and of *C. serialis* that have been given above are true for the great majority of hooks. Yet, as has been mentioned, variation amongst the hooks sometimes obscures their distinguishing features. For example several small hooks of *C. cerebralis* have been found with short dorsally curving handles, so that if they had been isolated when examined they would have been diagnosed as small hooks of *C. serialis* as in this Coenurus the majority of small hooks have dorsally curving handles.

In my material the tissue of the cyst from the rat and of that of *C. cerebralis* contained numerous calcareous bodies, but they were absent in both cysts of *C. serialis*. Hall says that in his examples of adult *Taenia serialis* the calcareous bodies were extremely abundant.

From the data given above it is evident that the Coenurus from the rat is either a new species or a very atypical form of a known species. A more definite conclusion than this is impossible owing to the scantiness of necessary material.

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SOME FACTORS IN PLANT COMPETITION.

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(With 10 Text-figures and Plate V.)

One of the commonplaces of agriculture and horticulture is that when plants of the same or different species grow in juxtaposition a mutual influence is exerted which is known as "competition." Every plant needs a certain definite supply of such essentials as food, water and light to enable it to reach its full development, and when other individuals with similar requirements are in the near neighbourhood they encroach upon these supplies and a sharp struggle for existence is the outcome. This fact of competition is fully recognised by every practical man, and much nicety of judgment is often exercised to give a crop adequate room for reasonable development in order to obtain the largest yield possible from a given area of land. It is not always an economic policy to give each plant the space it needs to attain its maximum growth, as the individuals may benefit at the expense of the total crop. Under certain circumstances, however, this policy of eliminating competition as far as possible is markedly successful, as in the case of wheat growing in the droughty districts of China[1]. The wheat is planted in "hills" arranged in double rows spaced widely apart, the hills being 24 to 26 inches from centre to centre, the rows 16 inches apart, and the space between each pair of rows 30 inches. In an unusually dry season a yield of 12 bushels per acre is obtained by this method, whereas in a very favourable season (as 1901) as much as 116 bushels[2] has been reported for small areas. Without this very specialised method of cultivation in these districts it would be impossible to obtain a wheat crop at all, but in most places with larger rainfall the end would not justify the means. A good many experiments have been carried out on thick versus thin seeding of cereals, wide versus narrow drills, etc., the results varying with locality and season. It is, however,

[1] King, F. H., *Farmers of Forty Centuries*, pp. 239–242.

[2] There is no evidence to show the weight per bushel in this case.

generally recognised that up to a certain point it is profitable to give growing crops plenty of room, but that beyond this limit the total yield is apt to fall off.

Up to the present time most of our knowledge of competition has been purely empirical and derived from observation and deduction from plants grown under various cultural conditions not under strict control. Consequently little information is available as to the relative importance of the different factors that come into play when one plant enters into competition with another, or of the interaction between these factors. During the past five years a number of experiments have been carried out at Rothamsted which aimed at isolating some of the more important of these factors, and establishing their relationship to the growth of the plant. A full discussion of the problem will not be possible till far more data have been accumulated, but a preliminary account will indicate the present position of the work.

"Competition" of one plant with another is a very complex, not a simple, phenomenon, and may be broadly analysed as follows:

(1) Competition for food from the soil.

(2) Competition for water.

(3) Competition for light.

(4) The possible harmful effect due to toxic excretions from the roots, if such occur.

The first three factors lend themselves to direct experiment; the fourth is more difficult to demonstrate but the possibility of its existence must be reckoned with in estimating results.

1. GENERAL COMPETITION.

(*Including* 1, 2, 3 *above at the same time.*)

Pot cultures were carried out with mustard and barley, glazed earthenware pots being used, each holding 10 or 20 kilos of soil. The soil was obtained from an unmanured area on Great Knott Field, Rothamsted, sifted, and mixed with 10 per cent. sand to lighten it before use. No manures were added in any case, so that the only mineral food available for the plants was that present in the soil at the beginning of the experiment. The seeds were sown in double quantity, but as soon as germination was established the seedlings were thinned out to the correct number per pot. All seedlings thus removed and any weeds that put in an appearance were laid on the surface of the soil in order to avoid removing any of the original food supply and so altering the

balance between the pots. Watering was done regularly, a similar quantity being given to every pot on each occasion, so that the amount of water available during the progress of the experiment was the same in every case.

Varying degrees of competition were induced by variations in the rate of seeding, from one to five plants being raised in the narrow pots containing 10 kilos of soil, and from one to eight in the broad pots with 20 kilos of soil. The pots were arranged in groups of five or eight (one pot of each rate of seeding per group) and the groups were scattered over the glasshouse on trucks to equalise conditions. When growth was well established and the weather was favourable the trucks were run outdoors into a wire cage. Mustard and barley were both tested, 10 narrow pots or 3 broad pots being used as a unit in every case.

Experiment I.

Mustard.

Narrow pots, 10 kilos soil.
Seeds sown March 31st, 1917. One to five per pot after initial thinning.
Plants cut May 29th, 1917.

Very soon after the plants had emerged from the seedling stage it was evident that the strength of development was in inverse ratio to the number of plants per pot, and this relation became more and more marked as time went on. The mustard was cut while most of the plants were in full flower, though some had begun to go over into fruit. A definite gradation of maturity occurred according to the number of plants in the pot. The *single plants* (per pot) were very strong, sappy, exceedingly tall and decidedly less mature than any others. The lower leaves had begun to turn yellow but were not at all wilted and none had dropped off. In most cases only the lowest flowers were fully developed, the upper ones being in various stages of bud, while the axillary racemes had hardly any flowers open. The *five plants per pot* were of medium strength only, comparatively short, with stems inclined to be woody, and were the most mature of all. The lower leaves had wilted and in many cases had dropped off, so that they had to be gathered up for the purpose of weighing. The flowers were fully out, and many on the main stem had begun to form fruit.

The 2, 3, 4 plants per pot showed a steady gradation between the two extremes of 1 and 5 plants per pot.

Table I.

Average results per pot (average of 10 pots).

No. of plants	Green wt. gm.	Dry wt. gm.	% dry in green	Water present gm.	% N in dry	Actual N gm.
1	44·40 ± 1·12	7·88 ± ·22	17·93 ± ·64	36·52 ± ·9	1·84	·144 ± ·004
2	43·05 ± 1·54	8·24 ± ·26	19·30 ± ·54	34·81 ± 1·28	1·77	·145 ± ·005
3	42·03 ± 0·90	8·69 ± ·13	20·83 ± ·42	33·34 ± ·77	1·66	·144 ± ·003
4	36·55 ± 0·91	8·17 ± ·36	22·32 ± ·26	28·38 ± ·55	1·62	·132 ± ·005
5	39·08 ± 1·07	8·53 ± ·18	21·92 ± ·31	30·55 ± ·89	1·57	·134 ± ·005

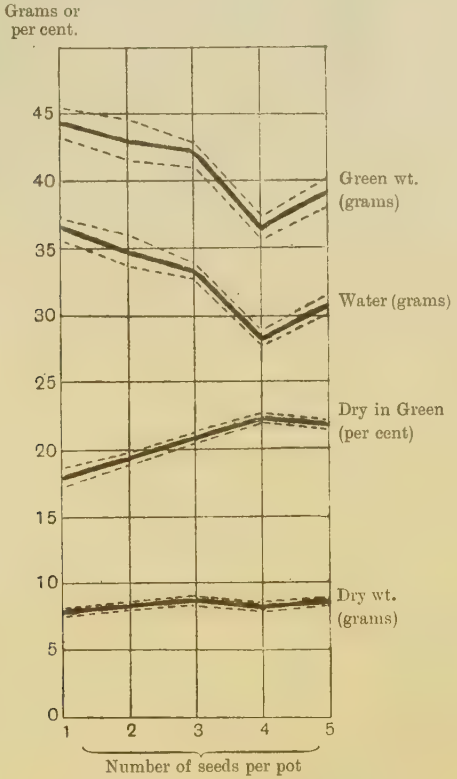

Fig. 1. Curves showing the amount of green weight, dry matter and water (in grams) and the percentage of dry matter in green weight when varying numbers of mustard plants were grown in 10 kilos of soil (tall pots).

The average results for the ten pots with each rate of seeding are set out in Table I and Fig. 1. The quantity of dry matter produced per pot is practically identical in each case, as the variations fall within the limits of experimental error. This indicates that the nutritive functions are severely limited by some factor of competition which cuts down the normal activities of the plants in proportion to the number of individuals that are struggling for existence in a similar bulk of soil. With 1, 2, or 3 plants per pot the amount of nitrogen taken up is identical, and it is evident that the whole of the nitrogen available for use as food was used by a single mustard plant under the conditions of experiment, and where more plants were grown per pot the individuals were unable to obtain as much as they could utilise. Probably therefore, the chief competitive factor in this case was the quantity of available nitrogen, as when once this was all absorbed the plants were unable to make further use of other nutritive substances. With 4 or 5 plants per pot, on the other hand, the whole of the available nitrogen was not taken up, the quantity lacking being slightly outside the limits of experimental error. At the same time a sharp drop occurred in the green weight, due entirely to the presence of less water, the dry weights being almost constant. In this case some other limiting factor, probably not nutritive, was apparently beginning to come into action, but the available data at this stage do not allow of any certainty as to its nature. With 4 or 5 seeds per pot the plants matured very much earlier, and by the time of cutting a considerable amount of desiccation had already occurred, which would account for the drop in water content but not for the reduced intake of nitrogen, both in actual weight and in proportion to the total dry matter.

The amount of water supplied to the pots was the same in every case, and the amount of dry matter formed per pot was constant, irrespective of the rate of seeding. Nevertheless the plants made very different use of the water, the thinly seeded plants retaining far more in their tissues, so that the succulence as shown by per cent. dry matter in green weight decreased steadily as the plants became more crowded, from 1 to 4 or 5 per pot, 4 and 5 per pot being alike in this respect. This is not merely a question of the quantity of water available for use by individual plants, as with constant supply and constant dry matter it would be theoretically possible to attain a similar degree of succulence in each case, but the interplay of the various factors of competition is such that the balance of the physiological processes is altered as crowding occurs and the response is partly in the direction of change of succulence.

On the whole, therefore, it is apparent that where a number of plants are growing in close association with a limited supply of food the quantity of available nitrogen sets a definite limit to the possible growth, and so is a very important factor in the competition between plants. Other factors are in play, however, and later experiments were designed to isolate the more important of these (see p. 151).

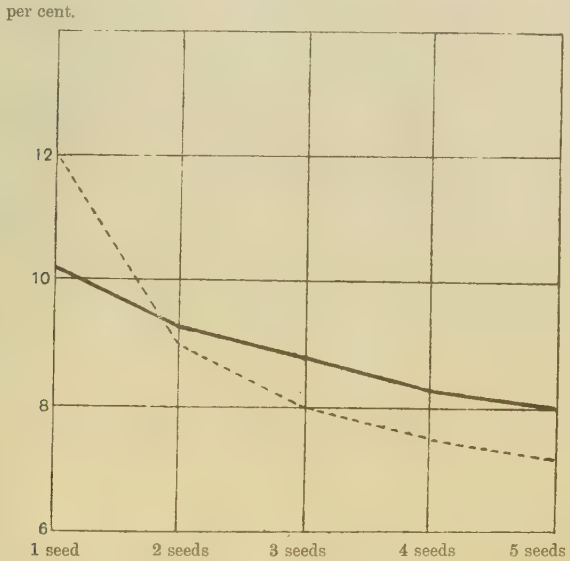

Fig. 2. Black line shows the efficiency index of dry weight production (per cent.) when varying numbers of mustard plants were grown in 10 kilos of soil (tall pots).

Dotted line shows the relative amount of food available per plant with each rate of seeding.

V. H. Blackman has recently put forward an important proposition indicating that the growth of an annual plant, at least in its early stages, follows approximately the "compound interest law[1]," the rate of interest or the percentage rate at which plant material accrues being termed the "efficiency index" of dry weight production. In the present experiment the reduction in the amount of dry matter produced by each individual plant with a decrease in the supply of available food is an expression

[1] Blackman, V. H. (1919). "The compound interest law and plant growth." *Ann. Bot.* XXXIII, p. 357.

of the alteration in the efficiency index, as the working capacity of the plant in this case is limited by the material with which it can build up its tissues.

Table II. *Efficiency indices for* 10 *pots.*

Mustard.

	Range per cent.	Average efficiency index per cent.
1 seed per pot	10·5 —9·843	10·19
2 „ „	9·475—8·895	9·247
3 „ „	8·91 —8·558	8·734
4 „ „	8·558—7·91	8·229
5 „ „	8·161—7·796	7·969

Table II and Fig. 2 show graphically the steady fall in the efficiency index as the food supply gets less. The close correlation of cause and effect is shown by the dotted curve which represents the relative actual food supply per plant. Though the steepness of the curves varies, especially in the initial drop from 1 to 2 seeds, the direction changes in the same sense in every case, as the one factor follows in the wake of the other.

Experiment II.

Barley.

Narrow pots. 10 kilos soil.
Seeds sown March 21st, 1917. One to five per pot after thinning.
Plants cut July 16th, 1917.
Broad pots. 20 kilos soil.
Seeds sown March 21st, 1917. One to eight per pot after thinning.
Plants cut July 16th, 1917.

This test resembled Experiment I, but was carried out with a different plant, barley, to ascertain whether the response to competition was similar in two widely varying species. Two sizes of pots were used in this case in order to obtain further evidence of the correlation between the amount of growth and the quantity of available food.

From an early stage in the experiment the strength of the individual barley plants varied inversely as the rate of seeding, though the superiority of the thinly seeded plants was not so markedly evident as in the case of mustard. The same relative position was maintained to the time of harvesting, when the thinly seeded plants were better developed and much less mature than the more crowded specimens. In all cases the lower leaves were ripe and brown, but the ears varied considerably in maturity from greenish grains with green awns (1 plant per pot) through

various stages of yellow coloration to dead ripe grains with dull brown awns (5 plants or 8 plants per pot). In the single plants the straw was thick, the leaves broad and well developed and the ears rather numerous, and these plants were also rather taller than any of the others. As the number of plants increased the stems became thinner, the leaves narrower and the ears fewer, and in all cases the more crowded the plants the more mature they were. This hastening of maturity is probably associated with the varying quantity of water available per plant, as it is well known that in a dry season when little water can be obtained cereals and other crops ripen off more rapidly in response to the drought.

Table III. *Average results per narrow pot (average of 10 pots).*

No. of plants	No. of ears	Green wt. gms.	Dry wt. gms.	% dry in green	Water present gms.	% N in dry	Actual N gm.
1	9·1	56·77 ± 2·72	25·86 ± 1·09	46·28 ± 1·04	30·91 ± 1·63	·776 ± ·016	·199 ± ·0068
2	10·4	58·09 ± 1·47	27·22 ± ·35	47·29 ± ·90	30·87 ± 1·12	·748 ± ·010	·203 ± ·004
3	11·5	55·10 ± 1·43	26·98 ± ·61	49·07 ± ·65	28·12 ± ·82	·766 ± ·009	·207 ± ·005
4	11·3	51·99 ± 1·69	26·05 ± ·50	50·91 ± 1·36	25·94 ± 1·19	·771 ± ·009	·201 ± ·003
5	12·8	57·76 ± 1·12	27·87 ± ·37	48·38 ± ·44	29·89 ± ·75	·734 ± ·010	·204 ± ·003

Table IV. *Average results per broad pot (average of 3 pots).*

No. of plants	No. of ears	Green wt. gms.	Dry wt. gms.	% dry in green	Water present gms.	% N in dry	Actual N gm.
1	14·3	125·97	51·64	40·88	74·33	·778	·3998
2	16·3	108·53	49·66	45·76	58·87	·783	·4162
3	19·3	115·03	52·33	45·59	62·70	·744	·3881
4	20·0	116·76	53·69	42·76	63·07	·771	·4141
5	19·0	106·89	52·15	49·05	54·74	·809	·4219
6	20·0	109·07	52·55	48·15	56·52	·759	·3982
7	23·0	109·46	53·29	48·86	56·17	·753	·4014
8	24·0	105·34	51·16	48·57	54·18	·792	·4050

In the narrow pots the numerical results were very similar whatever the rate of seeding, except that rather more ears were produced per pot with an increase in the number of plants. The actual amount of nitrogen extracted was practically identical in each case, again indicating that the amount of available nitrogen was one of the chief, if not the chief, factors in determining the amount of growth. The results obtained with the broad pots were much the same. The amounts of dry matter produced and the nitrogen extracted showed little variation from set to set, but were just twice as great as in the narrow pots, as twice the

amount of soil and therefore twice the quantity of plant food was available. This affords yet more conclusive evidence that under the conditions of this experiment the amount of growth possible was strictly dependent on the available nitrogen, irrespective of the number of plants. A comparison of the figures for individual plants (Table V) shows that the amount of dry matter produced and nitrogen extracted is practically proportional to the amount of soil available and therefore to the quantity of plant food, especially nitrogen, and also that a given quantity of soil only admits of a given amount of growth.

It is interesting to notice that while barley was able to extract ·20 gm. N from each tall pot, mustard only took away ·14 gm. This may be due to the longer period over which the barley was grown, or possibly to some essential difference in the absorptive action of the two plants.

Table V.

Broad pots				*Narrow pots*			
No. of plants per pot	Green wt. per plant gms.	Dry wt. per plant gms.	Total N removed per plant gms.	No. of plants per pot	Green wt. per plant gms.	Dry wt. per plant gms.	Total N removed per plant gms.
* 2	54·26	24·83	·2081	1	56·77	25·86	·1990
4	29·19	13·42	·1035	2	29·05	13·61	·1017
6	18·18	8·76	·0664	3	18·37	9·00	·0688
8	13·17	6·39	·0506	4	13·00	6·51	·0502

* As the broad pots contained twice as much soil as the narrow ones, each plant in the broad pots with 2, 4, 6, 8 plants had the use of the same amount of soil as 1, 2, 3, 4 plants respectively in the narrow pots.

Table VI. *Efficiency Indices. Barley.*

For 10 *tall pots.*

	Range	Average efficiency index
1 seed per pot	5·419—4·966	5·258
2 „ „	4·796—4·578	4·712
3 „ „	4·431—4·023	4·358
4 „ „	4·151—3·927	4·080
5 „ „	4·021—3·858	3·948

For 3 *broad pots.*

1 seed per pot	5·933—5·708	5·852
2 „ „	5·305—5·055	5·225
3 „ „	4·952—4·876	4·922
4 „ „	4·712—4·674	4·701
5 „ „	4·536—4·431	4·483
6 „ „	4·382—4·254	4·334
7 „ „	4·256—4·190	4·214
8 „ „	4·163—4·130	4·147

The association between the amount of growth and the quantity of soil available is further demonstrated by the efficiency indices of the barley with different rates of seeding (Table VI), the index decreasing steadily with the increase in the number of seeds per pot. Fig. 3 shows this even more strikingly. As the large pots contain exactly twice as much soil as the narrow pots, two seeds in large pots each have as much soil and therefore food available as one seed in the narrow pots, four in large as two in narrow, etc. Consequently in the figure the efficiency indices for both sets of pots are plotted together according to the quantity of soil available for individual plants, and the curves are practically coincident, showing again how entirely dependent the growth is on the available food supply.

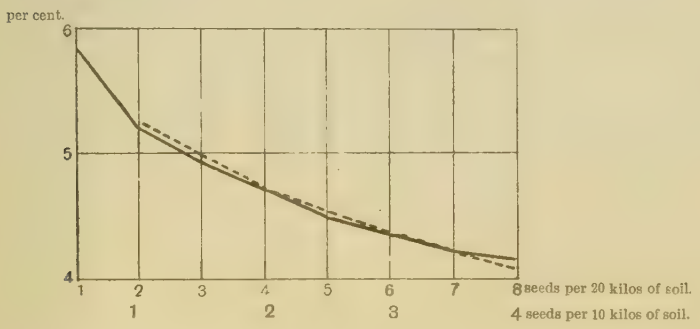

Fig. 3. Black line shows the average efficiency indices for varying numbers of plants grown in 20 kilos of soil (broad pots).
Dotted line ditto in 10 kilos of soil (tall pots).

2. EFFECT OF INDIVIDUAL FACTORS ON COMPETITION.

The above experiments with mustard and barley show that if the food supply in the soil is restricted this will be the chief limiting factor in determining the amount of possible growth, and therefore the action of other factors of competition will be less obvious. On the other hand, these other factors are at work at the same time under these conditions so that the results obtained are not necessarily solely due to competition for food. In order, therefore, to ascertain the working of the various factors it is necessary to arrange experiments in which each may be studied individually, without interference by the others.

A. Influence of food supply on competition.

Proof of the close relation between the quantity of available food and the amount of growth made was obtained from several sets of water cultures carried out with barley and wheat in 1915. The plants were grown in four food solutions of different strengths, the usual culture solution[1] (called N for convenience) and others one-fifth, one-tenth, and one-twentieth as strong $\left(N, \frac{N}{5}, \frac{N}{10}, \frac{N}{20}\right)$. Each experiment (three in all) was carried on for six weeks, three series being run at the same time. In one the nutrient solution was changed every four days, in the second it was changed once (half-way through the test), and in the third no change was made at all. The plants were spaced at equal distances apart, so that each received a similar light supply. In every case it was found that the dry weights of the plants decreased coincidently with the strength of the nutrient solution. Even where the solutions were constantly changed the $\frac{N}{20}$ or $\frac{N}{10}$ plants were very much behind the N plants, showing that the total quantity of available food had a direct bearing on the amount of growth. When the solutions were changed but once, or not at all, the $\frac{N}{5}$ plants were considerably weaker than the N, as they had apparently not received as much food as they could deal with. When the solutions were frequently changed, however, the $\frac{N}{5}$ plants did not fall nearly so much behind the N, indicating that the total amount of food supplied in the solution with constant changing enabled the plants to make almost their maximum growth, while the N plants probably received more food than they could profitably deal with[2]. (Fig. 4.)

Thus, when the competition of one plant with another for food is removed, and when the water supply is adequate and all plants receive a similar and plentiful supply of light, it is seen that up to a certain limit the amount of growth is proportional to the supply of food, though

[1] Potassium nitrate 1 gm.
Magnesium sulphate ·5 „
Calcium sulphate ·5 „
Potassium di-hydrogen phosphate ·5 „
Sodium chloride ·5 „
Ferric chloride ·04 „
Distilled water—to make up 1 litre.

[2] Brenchley, W. E. (1916). "The effect of the concentration of the nutrient solution on the growth of barley and wheat in water cultures." *Ann. Bot.* xxx, 77–90.

above that limit the plants are unable to make full use of their supply. This, then, may be regarded as an argument for giving crops a fair amount of room in order that they may obtain sufficient food, though too thin planting may be wasteful as the plants may be unable to make the best use of the available food.

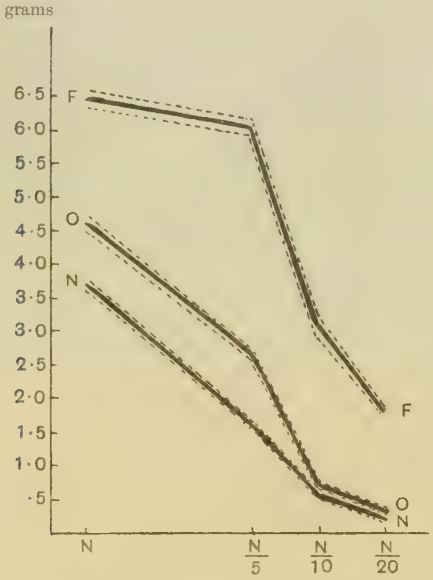

Fig. 4. Average dry weights of ten barley plants grown in water cultures in nutrient solutions of different concentrations. Dotted lines show limits of probable error.

F. Solutions changed every four days.

O. Solutions changed once during experiment.

N. Solutions never changed.

B. LIGHT AS A FACTOR IN COMPETITION.

Although it is always stated that overcrowding of plants leads to great competition for food and light, still little or nothing is definitely known as to the extent to which competition for light affects the growth of plants. As overcrowding increases, both factors come more and more into play, and under ordinary cultural and experimental conditions it is impossible to separate the two and to attribute any proportional action to one or the other. The first experiments described above (pp. 144–151)

showed clearly how powerful a factor a limited food supply is, but no evidence was obtained as to the action of the light factor. To elucidate this point water cultures were set up in which no shortage of food or water was allowed to occur, but in which the light supply was varied by the conditions of spacing. Sixty-four barley plants were placed separately in nutrient solution and the bottles were packed in a square with eight plants per side, as closely as possible, the distance from plant to plant being $3\frac{1}{2}$ inches. Another 64 bottles, each with its plant, were arranged on the greenhouse benches in the immediate vicinity of the crowded set, but in this case each bottle was at least one foot away from its nearest neighbour. Each bottle was kept in the same place throughout the experiment, the nutrient solution being constantly changed to prevent any lack of food or water introducing another factor of competition. In this way it was hoped to obtain conditions of dense overcrowding on the one hand, and absolute freedom from light competition on the other, and the result justified the means.

For the first five or six weeks, while the barley plants were quite small and no overlapping of leaves occurred no difference was observed in the growth of the spaced and crowded plants. As tillering began, the crowded plants gradually seemed to improve more rapidly than the spaced ones, though for some time it was doubtful if this were not merely an optical illusion. After eight weeks' growth it was obvious that the crowded plants were really the better. The leaves were decidedly larger and broader, of a much darker green, while the spaced plants were narrower in leaf and of a lighter yellowish colour, some plants showing a tendency to chlorotic stripes. At this stage a wet and dry bulb thermometer was inserted amongst the leaves of the crowded plants, and another was placed in the greenhouse away from the foliage. The difference rapidly became still more marked, and a week later photographs were taken (Plate V, figs. 1 and 2).

For the sake of a fair comparison the spaced plants were temporarily crowded together (Plate V, fig. 2) in order to avoid giving the crowded plants an unfair advantage due to optical illusion.

A little later the succulence of the crowded plants was very noticeable, the texture recalling that of marsh plants. The stems were very fleshy and the plants, especially in the middle of the square, had begun to depend upon their neighbours for support. The spaced plants at this time appeared to be rather more tillered, and the tillers took full advantage of the available space and spread out in rosettes on the tops of the bottles. The leaves and shoots were much tougher and less easily

Fig. 1. Photo. of spaced and crowded barley plants as they stood during experiment. Crowded set at back on left, spaced plants in foreground.

Fig. 2. Photo. showing spaced barley plants temporarily placed close together for comparison with those that were permanently crowded during experiment. Crowded set on left, spaced set on right.

broken than those of the crowded set. About this time or a little earlier differences began to manifest themselves between the plants in the various parts of the crowded square. Those in the outside rank were well tillered, with plenty of good strong healthy leaves, but as the middle of the square was approached the number of tillers began to grow less and the plants became lanky, thin, and much less healthy. At this stage the assistant who constantly handled the plants in changing the solution expressed the opinion that the spaced plants would probably prove better in the long run than the crowded plants, in spite of the broad hefty leaves of the latter, an opinion that later events proved to be justified.

All the plants began to show ears at about the same time, in spite of the various differences in maturity of the two sets. The spaced plants were looking very unhappy, as the lower leaves changed colour and died down badly, while the tillers were not nearly as tall as in the crowded set. The crowded plants, on the other hand, retained their dark green colour, and although maturity was much less advanced as regards vegetative growth the ears were fully as advanced as in the spaced set. The ocular difference between the two sets reached its zenith at this time, the contrast between the narrow yellowish withering leaves of the spaced plants and the broad dark-green succulent leaves of the crowded ones being most striking. A few days of excessive heat supervened at the end of the experiment and all the plants showed the effect. Almost all the leaves of the spaced set ripened off, and were yellow and withered, but the plants were well tillered, with stout dry stems and well-developed ears. Little mildew was present though a good deal of aphis was about. The leaves of the crowded plants had also begun to die off, but became flaccid and reddish instead of being rather stiff and yellow. The ear and grain formation of the outer plants of the square were ahead of the spaced set, but the middle plants showed little fructification and were becoming slimy at the base of the stems, which were sappy and easily bent. Mildew was much more prevalent but less aphis occurred than on the spaced plants.

At this stage each plant was taken off, the roots were carefully washed in two changes of clear water to remove adherent food salts, and the dry weights were ascertained after several days drying in the drying room at a temperature of 80°–90° F. The number of ears and the number of stalks per plant were counted before cutting up.

The comparison of the spaced and crowded plants at various stages of growth and after drying yields several interesting and rather

surprising results. According to the usual conception of things dense overcrowding produces thin, unhealthy plants, badly drawn up, with few and small leaves often of a bad colour, whereas plants with plenty of space become stout and stocky, with a large area of healthy leaves. In the present instance overcrowding was apparently favourable to growth for some long period, as the plants became so much larger, with very broad leaves of an intensely dark colour, while the corresponding spaced plants were considerably smaller, with narrow pale leaves, which tended to die off at a rather early stage. The reason for this reversal of the usual order of things is not obvious, but certain suggestions may ultimately throw some light upon it. The experiments were carried on in a roof greenhouse which receives plenty of sun and tends to become very hot at times. The range of temperature during the course of the experiment is shown in Table VII.

Table VII.

1919	Maximum	Minimum
March 1—31	44°— 72° F.	26°—52° F.
April 1—30	64°— 95°	32°—52°
May 1—31	64°—110°	32°—56°
June 1—20	68°— 99°	40°—59°

Strong sunlight tends to check growth to some extent, and as the spaced plants were each so far separated from their neighbours as to permit of no shading, the insolation had full play and possibly kept back leaf development. The strong light may also have had some effect upon the chlorophyll, preventing it from attaining a very deep colour. The crowded plants cast considerable shade on one another thereby reducing the insolation, and this may have enabled the plants to form longer and broader leaves as growth was less checked by the light, while the chlorophyll developed a very full deep colour. The amount of shading, however, did not seem to be sufficient to account for the marked difference in external appearance, and other factors were sought for. The wet and dry bulb thermometers which were kept in the house and among the crowded leaves showed that except on rare occasions the humidity of the air among the crowded plants was greater than that in the free air of the house. The range of variation was very considerable, reaching to as much as 50 per cent. saturation, as is shown in Table VIII.

The character of the crowded leaves suggests a correlation with this difference of humidity. The succulence and slight fleshiness of these leaves recalls those of plants growing in very moist places, in marshes or

by water, where the air is naturally always moist even in hot weather, while the dry harsher leaves of the spaced plants may well be correlated with the relatively low humidity of the air with which they are surrounded. The marked difference in humidity might not occur out of doors where there is a freer circulation of air than in a greenhouse, and the absence of this extra moisture when plants are crowded in the field may account for the fact that the excessive leaf growth in barley under these conditions is not a usual occurrence. The extra growth of the crowded plants at this stage is not caused by a higher temperature among the leaves, as almost every day the dry bulb in this position registered a *lower* temperature than that exposed to the free air of the greenhouse.

Table VIII.

Difference between humidity of house and humidity among plants. Percentage of saturation	Number of days difference was recorded
Humidity among plants *higher* than humidity of house.	
0—10	8
11—20	8
21—30	10
31—40	5
41—50	1
Total	32
Humidity among plants *lower* than humidity of house.	
0—10	4
11—20	2
21—30	1
31—40	1
Total	8

For several weeks it appeared as though, contrary to all accepted notions, the crowded plants were going to produce better plants and a larger crop than those that had had plenty of room. As has been already recorded, however, signs of deterioration gradually set in, especially among the plants in the middle of the square, and by the time the plants were cut marked differences were noticeable. The chief points of difference are noted under their several heads.

1. *Number of ears.* When the ears were counted half the crowded plants possessed none at all, while all the spaced plants but three had one or more, thirty-nine of them possessing from 6–8 ears apiece. *In toto* the 64 crowded plants only produced 178 ears while the 64 spaced ones had 362, more than double the number being formed when adequate

room for growth was available. The number of plants with various numbers of ears was as follows:

Number of plants with specified numbers of ears.

No. of ears per plant	Crowded plants	Spaced plants
0	32	3
1	3	3
2	2	3
3	4	6
4	3	5
5	3	1
6	4	13
7	4	14
8	4	12
9	3	3
10	1	—
11	1	1

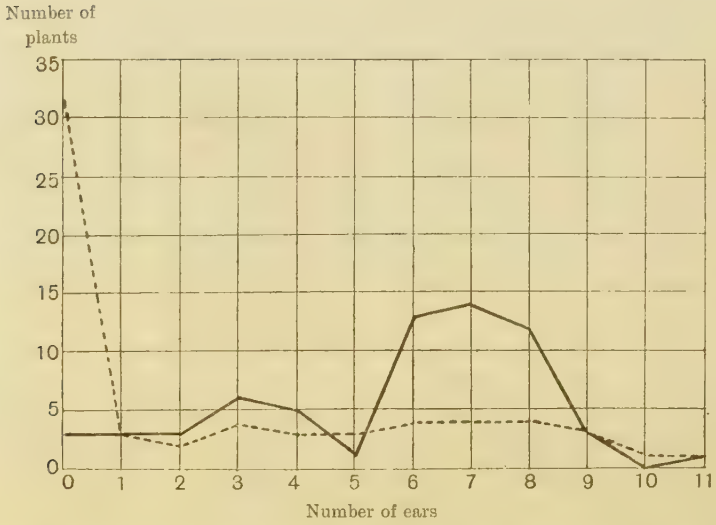

Fig. 5. Curves showing the number of barley plants with various numbers of ears when grown under conditions of (1) crowding, (2) adequate spacing. 64 plants in each set.
Black line—spaced plants.
Dotted line—crowded plants.

The above figures are graphically expressed in Fig. 5. As such a large proportion of the plants have from 6–8 ears this may be regarded as a standard type.

The spaced plants occupied a rather large area of bench in the green-

house surrounding the crowded square. The greater number of the plants which only formed a few ears (from 0–3) were grouped together at one end of the house which is occasionally slightly shaded by other parts of the structure. This concentration may be merely coincidence, or it may be due in some way to less advantageous conditions than the rest of the plants endured. The rest of the bench space was more equally illuminated, and the plants with similar numbers of ears were well

2	0	7	8	0	0	1	0
7	0	0	0	0	0	7	5
4	0	6	0	0	3	4	6
4	3	0	0	6	6	0	0
0	0	0	0	1	0	1	3
3	0	0	0	0	0	2	10
9	6	0	0	0	0	9	7
11	8	8	5	6	7	8	9

Fig. 6. Diagram showing the number of ears produced by each of 64 crowded barley plants in the positions they occupied during growth.

distributed and not grouped at all. In the crowded set the number of ears per plant depended very largely upon the position in the square. The majority (22 out of 28) of those in the outer rank produced ears varying in number from 1–11 whereas only 10 plants in 36 in the inner squares had any ears at all, from 1–9. The distribution is shown in the diagram (Fig. 6), which gives the number of ears for each plant occupying a certain position in the square.

The crowding, therefore, was very disadvantageous to the production of ears, and the paucity of fruiting stems in the inner parts of the square supports the idea that overcrowding in the field may have a very definite tendency to reduce the crop by weakening the plants below fruit bearing standard.

2. *Number of tillers per plant.* Apart from the ears produced the number of tillers thrown out by each plant is instructive. 62 out of 64 spaced plants had from 8–20 tillers and of these more than half possessed from 10–12 stalks, no plants showing less than 8. Overcrowding, however, tended both to decrease and increase the number of stalks, widening the range of variability in this respect. This suggests that when no competition for light occurred the plants tended towards the production of a standard number of stalks, whereas when competition was very keen each plant, in playing for its own hand, produced a number of stalks in accordance with the particular advantage or disadvantage it gained. (Fig. 7.)

With the spaced plants the position in the greenhouse had no bearing on the tillering, but in the crowded square the outside rank carried the largest number of stalks per plant, the second rank came a bad second, while the two innermost squares bore the smallest numbers of tillers, which were of a weakly character. In this respect the amount of tillering and ear formation ran parallel. (Fig. 8.)

Where the plants had sufficient space some correlation occurred between the number of tillers produced and the number of ears formed, but when they were crowded this correlation disappeared. In the spaced plants nearly all the plants with ears had 8–18 stalks, while the largest number of the standard 6–8 ears (see p. 158) were produced on plants with 10–14 stalks, very few being outside this limit, thus roughly speaking every other tiller bore an ear. Among the crowded plants most of those with 4–12 tillers bore no ears at all, the ears being usually produced by plants with 14–26 stalks, but no regular increase in the number of ears occurred with increased tillering. Adequate spacing, therefore, tends to reduce the number of tillers per plant that are necessary to produce a certain number of ears, and also causes a tendency towards a certain standard plant in which the number of tillers and ears formed vary within rather narrow limits. With overcrowding this standard plant disappears, and the amount of tillering gives no index of the number of associated ears.

3. *Comparative dry weights of plants.* The dry weights of the barley plants bore out the observations that adequate spacing tends to the production of a more even type of plant, while crowding accentuates

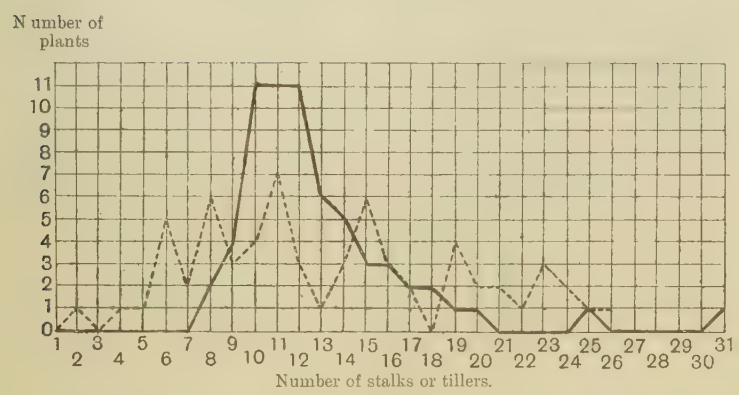

Fig. 7. Curves showing the number of barley plants with various numbers of tillers when grown under conditions of (1) crowding, (2) adequate spacing. 64 plants in each set. Black line—spaced plants. Dotted line—crowded plants.

25	11	19	14	24	21	15	23
23	7	11	6	8	11	14	20
18	11	8	8	8	9	15	17
24	19	7	8	6	10	9	21
26	10	11	2	11	6	6	23
19	11	5	6	4	12	10	15
15	17	14	12	9	8	13	15
12	10	16	19	20	22	15	16

Fig. 8. Diagram showing the number of tillers produced by each of 64 crowded barley plants in the positions they occupied during growth.

the difference between individuals and also prevents all the growth possible being made. The extreme range of weight is large even under favourable circumstances, but is greatly increased when the competition for light comes into play. The figures in Table IX show that this is the case with both the root and shoot, the extension of range in both cases being chiefly downwards owing to the hindrance to growth caused by crowding.

Table IX. *Total range of dry weights.*

	64 crowded plants gms.	64 spaced plants gms.
Shoot	·50—24·44	9·72—24·47
Root	·37— 5·57	1·52— 6·27
Whole plant	·97—30·01	12·34—28·74

The result of this downward range is to decrease the total amount of dry matter produced by a given number of crowded plants, and so to lower the average weight, as is shown in Table X.

Table X. *Total and average dry weights.*

	64 crowded plants		64 spaced plants	
	Total gms.	Average per plant gms.	Total gms.	Average per plant gms.
Shoot	778·89	12·17	1174·43	18·35
Root	123·32	1·92	256·58	4·01
Whole plant	902·21	14·09	1430·91	22·36

The total range and average weights, however, hardly give a fair picture of the general effect of overcrowding on the majority of the plants, and with such a large variation in weight the average is in reality of little value. A much clearer idea is obtained by a comparison of the interquartile range of the weights under the different conditions, as by this means the most abnormal plants, both large and small, are ruled out and only the more representative specimens come under consideration (Table XI).

Table XI. *Interquartile range (of 32 intermediate plants in each case).*

	64 crowded plants			64 spaced plants		
	Actual range gms.	Diff. gms.	Diff. Lowest wt of range	Actual range gms.	Diff. gms.	Diff. Lowest wt. of range
Shoot	6·07—18·59	12·52	2·06	16·54—20·54	4·0	·24
Root	·95— 2·82	1·87	1·97	3·47— 4·52	·85	·25
Whole plant	7·22—21·84	14·62	2·03	20·46—25·04	4·58	·22

These figures are far more instructive than those previously dealt with. They lay strong emphasis on the fact that overcrowding hinders even development whereas if sufficient room is available the plants tend in both root and shoot towards the production of a fairly uniform amount of dry matter—i.e. towards a more or less uniform growth. With overcrowding the difference between the greatest and least weight

19·12	11·07	24·11	23·31	19·27	12·94	14·34	20·12
21·84	11·10	8·69	3·29	5·94	6·29	15·20	22·21
23·02	7·94	13·94	5·84	5·90	10·16	14·81	19·71
23·06	14·66	4·79	6·19	5·39	7·44	8·77	15·04
18·29	6·32	9·54	0·97	9·89	6·07	5·82	21·44
13·74	7·04	2·64	3·74	2·92	10·59	11·17	23·67
26·11	23·11	9·47	10·34	8·49	7·22	23·76	22·97
30·01	19·70	26·87	23·91	19·27	21·96	23·51	25·86

Fig. 9. Diagram showing the number of grams of dry matter produced by each of 64 crowded barley plants in the positions they occupied during growth.

of the range is just twice the least weight, with shoot, root, and whole plant, whereas in the spaced plants the difference is so small that it only amounts to $\frac{1}{8}$ the least weight of the range, one eighth of that with the crowded set. This corroborates and justifies the statement made earlier in this paper that, other things being equal, in the absence of competition for light there is a tendency towards the production of a standard type of plant.

The actual effect of light competition on individual plants is clearly shown by the dry weight at different points of the crowded square. (Fig. 9.)

The plants in the outer rank are less subject to light competition than any of the others, as they are quite free and exposed on one side; most of these are fairly heavy, 14 out of 28 plants (50 per cent.) being above the upper limit of weight of the interquartile range, and none below it. The second rank suffers from the proximity of its healthy neighbours of the outer row, and is also flanked by others on the inner side, with the result that only 10 per cent. (2 out of 20) are above the upper limit and 35 per cent. (7 out of 20) are below the lower limit of the interquartile range. The third rank is worse still, with no heavy plants, but with 58 per cent. (7 out of 12) below the lower limit of range, while the innermost core of the square consists of four plants suffering most severely from the light shortage, 3 of them (75 per cent.) being below the lowest limit and the fourth not far above it. These results show more clearly when tabulated (Table XII).

Table XII.

		Above upper limit of interquartile range		Below lower limit of interquartile range	
	Number of plants	Number of plants	Percentage	Number of plants	Percentage
Outer rank	28	14	50	0	0
Second rank	20	2	10	7	35
Third rank	12	0	0	7	58
Fourth rank (inner core)	4	0	0	3	75

The depreciation in growth caused when even so small a number of plants as 64 are crowded is thus very great, and it is obvious that if the number were increased the total depreciation would be greatly augmented, as all the plants within the outer row or two of the mass would feel the effect of competition most severely. It is not a question of competition for food by the roots as every plant had its own individual supply which was never allowed to run short, but the competition for light prevented the inner plants from making adequate use of their mineral resources, and less dry matter was produced in consequence.

The physiological effect of this struggle for light finds morphological expression in the relations between the roots and shoots of the competing plants. In every case a full quantity of nutrients was supplied to the roots, but the amount of light available to carry on elaboration of sap and assimilation of carbon-dioxide in the leaves varied with the individual plant. When overcrowding occurred this implied a lessened

supply of prepared nutrient material for building up the tissues and it appears as if the plants attempted to dispose of this restricted quantity in order to combat the disadvantage as much as possible. With increased crowding the tendency is for the weight of the root to decrease more rapidly than that of the shoot, so that the shoot root ratio goes up. In other words, the plant tends to utilise a larger proportion of its elaborated food in laying down new leaf tissue, possibly in an attempt to increase its assimilatory surface in order to make the most of the diminished supply of light at its disposal. The corresponding reduction in root tissue is economic as it is useless for more dissolved mineral food to be absorbed than can be dealt with by the leaves. The range of variation in the shoot root ratio is greater with the crowded than with the spaced plants, corresponding again to the greater deviation of the competing plants from the standard type.

Table XIII. *Shoot/Root ratio.*

	Crowded plants	Spaced plants
Total range	1·064—13·57	3·005—8·482
Interquartile range	5·235— 7·906	3·98 —5·358

		Below lower limit of interquartile range		Above upper limit of interquartile range	
	Number of plants	Number of plants	Percentage	Number of plants	Percentage
Outer rank	28	11	39·3	5	17·8
Second rank	20	3	15·0	3	15·0
Third rank	12	1	8·3	5	41·6
Fourth rank (inner core)	4	1*	25*	3	75·0

* This plant was so abnormally weak in the shoot that it is not fair to include it in the consideration of the figures as the low shoot/root ratio in this case is simply due to the failure of the shoot to develop.

These figures of Table XIII lend numerical support to the idea that with increasing competition for light the growth of the shoot is made more and more at the expense of the root, so that the shoot/root ratio gets steadily larger. With an abundant supply of room, on the other hand, a more stable equilibrium is reached, a larger development of root in proportion to shoot occurs, and consequently the shoot root ratio is lower, particularly when the interquartile range is considered.

4. *Efficiency Index of dry weight production.* The efficiency index or rate of addition of dry matter of the individual plant shows more clearly than anything else how much the growth economy is affected by variation in the available light.

Table XIV. *Efficiency Index of spaced plants.*

	Range	Difference in range	
Total range	4·265—4·955	·690	
Interquartile range	4·678—4·842	·164	
First (lowest) quartile	4·265—4·662	·397	
Second quartile	4·678—4·777	·099	·264
Third quartile	4·790—4·842	·052	
Fourth (upper) quartile	4·842—4·955	·113	

The efficiency indices of the spaced plants cover a comparatively small range (Table XIV), while the interquartile range is very small. The lowest quartile includes all those plants which from one cause or another are weaker than their fellows, and the variation in efficiency of these plants is greater than that of all the rest. This indicates an approach to a certain standard of efficiency in the majority of the plants —i.e. that under the prevailing conditions in the greenhouse a certain quantity of growth is possible in the given time, and a large proportion of the spaced plants approximate to this standard. The increased deviation on the part of the minority may be due to the somewhat excessive insolation referred to earlier in this paper, which would tend to depress the growth of any plants that were naturally at all weakly. The variation in the rate of growth of the spaced plants may therefore be attributed to the different response of the individuals to their environment when they are not influenced by the proximity of other vegetation and are therefore free from competition.

The efficiency indices of the crowded plants reveal a very different state of affairs. The total range is very large, 2·199–4·989 per cent. per day[1]—and the interquartile range runs from 3·831–4·729, a far wider deviation than in the spaced plants. The average efficiency of the crowded plants as thus shown is lower than that of the others, and the approximation to the standard growth is considerably less.

Table XV. *Efficiency Index of crowded plants.*

	Range	Difference in range
Total range	*3·012—4·989	1·977
Interquartile range	3·831—4·729	·898
First (lowest) quartile	*3·012—3·811	·799
Second quartile	3·831—4·304	·473
Third quartile	4·353—4·729	·376
Fourth (upper) quartile	4·734—4·989	·255

* The index of the very weakly plant (2·199) is omitted.

[1] 2·199 is the index for the one exceptionally weak plant in the series, but even if this is rejected the range runs 3·012–4·989 per cent. per day.

An interesting feature is the very gradual closing up of the range of variation from the lowest (first) to the highest (fourth) quartile, when compared with the sudden change from the first to the second among the spaced plants.

4·623	4·178	4·809	4·784	4·630	4·304	4·388	4·664
4·729	4·179	3·980	3·190	3·672	3·719	4·436	4·741
4·772	3·908	4·365	3·658	3·665	4·118	4·416	4·649
4·774	4·406	3·496	3·705	3·593	3·855	3·990	4·426
4·585	3·723	4·057	2·199	4·086	3·689	3·654	4·718
4·353	3·811	3·012	3·295	3·095	4·142	4·185	4·795
4·877	4·777	4·050	4·123	3·962	3·831	4·799	4·771
4·989	4·649	4·898	4·807	4·629	4·734	4·790	4·869

Fig. 10. Diagram showing the efficiency index of dry weight production for each of 64 crowded barley plants in the positions they occupied during growth.

Table XVI.

	Total no. of plants	Lowest quartile 1st		2nd quartile		3rd quartile		Upper quartile 4th	
		No. of plants	%	No. of plants	%	No. of plants	%	No. of plants	%
Outer rank	28	0	0	2	7	12	43	14	50
Second rank	20	6	30	9	45	3	15	2	10
Third rank	12	7	58·3	4	33·3	1	8·3	—	0
Inner rank	4	3	75	1	25	—	0	—	0

Table XVI and Fig. 10 show that in the outer rank, where least competition occurs, 50 per cent. of the efficiency indices are in the highest and nearly all the rest in the third quartile. In the second rank where the competition is already rather great, the efficiencies vary considerably, being spread over the whole range with a heavy concentration in the two lowest quartiles. In the two innermost ranks, however, the efficiencies are very low, the larger percentage in each case being in the lowest quartile and none in the uppermost. These results prove graphically that, other things being equal, the degree of competition for light brought about by close spacing or crowding has a direct bearing on the efficiency of the plant in the production of new material. The greater the competition, the lower the efficiency, and consequently the lower the ultimate crop. Furthermore the balance of the plant economy is disturbed, and greater deviations from the standard type are induced, owing to the tendency to individual variation under similar conditions being encouraged and accentuated by the action of a competitive factor, which in this case is light.

5. *Nitrogen Content.* The total amount of nitrogen present in the spaced as compared with the crowded plants was 21·22 gms. against 18·22 gms., the larger total intake corresponding with the larger crop. The percentage of nitrogen, however, was lower in the spaced plants, being only 1·827 against 2·339. This implies that when the plants had sufficient space they were able to produce a larger amount of dry matter with a lower utilisation of nitrogen, and that although an abundance of nitrogen was supplied they did not make such inroads on it as would correspond with the excess of dry matter ultimately produced.

The difference in the degree of maturity of the two sets is reflected in the relative percentage of N in the straw and ears. Earlier work at Rothamsted[1] has shown that the percentage of nitrogen in the straw falls steadily from the time the grain begins to form, and that in the grain, after a slight initial fall, it rises steadily till maturity is reached. The spaced plants were much the more mature, and whereas the ears contained 3·432 per cent. N, the straw was so depleted that only 1·654 per cent. was present at the time of cutting. The crowded plants were still green and sappy, and the immigration from straw to ear was far less advanced, so that 2·273 per cent. N was still present in the straw, and the ears only possessed 2·959 per cent. Separate estimations were made for the different ranks of the crowded square, but no definite gradation

[1] Brenchley, W. E. (1912). "The Development of the Grain of Barley." *Ann. Bot.* XXVI, pp. 906, 917.

in nitrogen content was observed throughout. In the outer rank, though, in which ear formation was further advanced than in the interior of the square the percentage of nitrogen in the grain was higher than the average (3·02 per cent.) and in the straw was lower (2·08 per cent.) thus following the normal law.

The above experiment with spaced and crowded plants proves conclusively how potent a factor is light competition in determining the growth of plants. Under ordinary conditions of cultivation overcrowding inevitably reduces the food supply of the individual plants, and, as was shown in the early part of this paper, this itself sets a limit to the amount of possible growth. This is widely recognised, but the effect of deficient light supply is less self-evident and therefore less taken into account. When plants are crowded in the field the root range is less circumscribed than when they are grown in pots and the available food supply is less restricted. The harmful effect of overcrowding under such circumstances is therefore probably due less to deficient nutrition than to light starvation which can occur, as shown above, even when a full and abundant food supply is assured. Further work on this point is needed, especially with regard to broad leaved plants in which the degree of overshadowing of one plant by another is accentuated, and in which possibly the factor of light competition is therefore even more important than with such narrow-leaved plants as barley.

SUMMARY.

1. The mutual action of one plant on another when grown in juxtaposition, usually known as competition, is a very complex phenomenon. Among the factors which come into play are competition for food, water and light, and also the possible harmful effect due to toxic excretions from the roots.

2. When the food supply is limited the dominant factor of competition is that of food and in particular the amount of available nitrogen. Other things being equal the total growth as measured by the dry matter produced is determined by the nitrogen supply, irrespective of the number of plants drawing on the resources.

3. With limited food supply the efficiency index of dry weight production decreases with the number of plants, as the working capacity of the plant is limited by the quantity of material available for building up the tissues.

4. The decrease in light caused by overcrowding is a most potent factor in competition even when an abundance of food and water is presented to each individual plant. With barley the effect of light competition is

(*a*) To reduce the number of ears.

(*b*) To cause great irregularity in the number of tillers produced.

(*c*) To reduce the amount of dry matter formed.

(*d*) To encourage shoot growth at the expense of root growth, thus raising the ratio of shoot to root.

(*e*) To increase the variation in the efficiency indices of dry weight production of a number of crowded plants, lowering them on the average.

(*f*) To decrease the power of the plants to make use of the food supplied to the roots, as evidenced by the total quantity of nitrogen taken up by similar numbers of plants when spaced out and crowded.

5. With adequate illumination (in barley) there is a tendency towards the production of a standard type of plant in which the relation between the number of tillers and ears, dry weights, efficiency indices, and ratios of root to shoot approximates within variable degrees to a constant standard. With overcrowding this approximation entirely disappears.

A CONTRIBUTION TO THE LIFE-HISTORY OF THE LARCH CHERMES (*CNAPHALODES STROBILOBIUS*, KALT.)[1].

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(With Diagram and Plates VI and VII.)

INTRODUCTION.

The insect commonly known as Larch Blight from the conspicuous white "wax-wool" which it secretes on the leaves of this tree during the spring and summer months, possibly has the most complex life-cycle of any member of the family Chermesidae. The Genus Chermes was established as such under the family Phylloxeridae, and in course of time, with the increasing discovery of species, became included in a Sub-family Chermesinae, containing several Genera, and finally in a family, embracing the Sub-families Phylloxerinae and Chermesinae.

There may be justification for this, but it is suggested that such a classification is a little premature, considering that the Sub-family Chermesinae comprises as many as seven genera, containing altogether only about twenty species.

Further, as an example, the Genera Chermes and Cnaphalodes have been differentiated through petty structural and morphological characters, which pale in the face of the greater and more prominent differences in habit and structure of the various generations of a single species.

Finally, these genera have been founded without any reference to

[1] The greater portion of this Paper is the result of an investigation made for the Delegacy of Forestry at Oxford University in 1913 and 1914. A report, embracing the material in detail, was submitted to the Delegacy in June, 1914, but does not appear to have been published.

the sexual individuals, descriptions of which, indeed, seem to be entirely lacking in the voluminous literature [1] on the structure and classification, and in the majority of cases without anything like a complete knowledge of the life-histories.

The establishment of a new Genus for nearly every new species which comes to hand can surely be but a hindrance rather than a help to a sound systematic classification in the future.

Two species of Chermes in Great Britain are known to inhabit Spruce and Larch, respectively, as their host and intermediate host. Both form galls on Spruce and migrate to Larch by means of a winged parthenogenetic generation, and again return to Spruce by a similar winged generation, which, however, is different in details of structure and habit from the former.

Both these insects have received much attention recently, and an outstanding paper by Mr H. M. Steven, entitled "Contributions to the knowledge of the family Chermesidae," has been published in the *Proceedings of the Royal Society of Edinburgh*, vol. XXXVII, Part III, No. 21, June, 1917.

This paper supplies much information upon the life-cycles of the two Chermes mentioned, namely *Chermes viridis*, Ratz., and *Cnaphalodes strobilobius*, Kalt., and also upon the species of Cholodkovsky, which are confined to the Spruce only. It may be stated here that no discussion is advisable as yet upon the probability of the latter two species being identical with, and forming a phase of the life-history of, the two first-named species.

With regard to the nomenclature of the generations in the Chermesidae, the terms applied to two only have been used constantly since 1878, namely the *Fundatrix* and the *Sexuales*. The term *Sexupara* has been in general use since 1889, but the names given to the other winged, and wingless generations which deposit their eggs on the intermediate host-tree have undergone constant changes.

Mr Steven has again revised the terms for the latter in his paper, and the establishment of the names *Gallicola migrans*, and *Gallicola non-migrans* for the winged forms emerging from Spruce galls, and *Colonici sistens* and *progrediens* for the Larch generations, is admirable.

In the present paper, it is proposed to give a detailed description of the parthenogenetic cycles on the Larch, but for the sake of clarity, a brief summary of Mr Steven's work on the Spruce cycle is recalled.

[1] Except in Paul Marchal's paper, *Annales des Sciences naturelles* (*Zoologie*), 9th series, vol. XVIII, 1913, where a few figures of Sexuales of the genus Pineus only are given.

I. THE SPRUCE CYCLE.

The winged *Sexupara*, flying from Larch, lays 5–10 yellow-brown eggs on the older needles of Spruce in June, under a considerable covering of wax-wool.

The male and female *Sexuales* hatching from these moult four times each, and, having reached the adult wingless stage, the female lays a single fertilized egg during the second half of July.

A *Fundatrix* larva hatches from this straw-coloured egg in August, secretes wax-wool and hibernates until the following April. Having moulted three times, the wingless adult *Fundatrix* lays 50-100 eggs under much wax-wool on a weak bud.

These eggs are at first yellow, but later become greenish-brown. Larvae of the *Gallicola migrans* hatch from them, and, together with their *Fundatrix* mother, convert the Spruce bud into a "gall." The larvae undergo three moults within the gall, which opens from the beginning to the middle of July; they emerge as the fourth stage nymph, and a final moult gives the winged adult *Gallicola migrans*, which flies to Larch.

II. THE LARCH CYCLE.

The *Gallicola migrans* lays 20–40 dark brownish-green eggs on a Larch needle, under a very sparse wax-wool covering.

Individuals emerging from a gall on June 14th, 1913, at Oxford, were transferred to young Larch, where they finished ovipositing on June 19th. The larvae hatched from these eggs on July 1st.

A cluster of eggs collected from Larch in Hertfordshire on June 12th, 1919, hatched from June 20th–23rd.

THE COLONICI GENERATIONS.

All larvae hatching from the latter were of the *Sistens* form, and were active at first, but later settled on the bark of shoots and went into hibernation (Plate VI, Fig. 1).

In the following spring the larvae started feeding (Fig. 2), and were observed to undergo the first moult on April 9th, 1914 (Fig. 3), the second on April 15th (Fig. 4), and the third and last on April 20th (Fig. 5). The adult *Sistens* is wingless (Fig. 6) and, according to Mr Steven, lays 5–12 eggs a day, until 35–50 is reached, from March till the middle of May. The eggs are at first yellow, then bronze-green, and hatch into two kinds of larvae, (1) *Progrediens* (Plate VII, Fig. 7) and (2) *Sistens*, the latter being in the minority, and many of them appearing to die soon after hatching. The survivors appear to hibernate.

The *Progrediens* larvae climb onto the Larch needles, and start to suck, causing a bending of the leaf.

After two moults at intervals of seven days (Fig. 8), these larvae become divergent in structure in the third stage, one portion (*a*) remaining elongate and slim (Fig. 9), and the other (*b*) becoming oval and stout (Fig. 12). After a third moult, the former (*a*) become nymphs (Fig. 10), and after a fourth and last, at the beginning of June, the winged adult *Sexuparae* (Fig. 11), which fly to Spruce and produce the *Sexualis* generation. The stout third-stage larvae (*b*) secrete a small amount of wax-wool, then moult for the last (third) time, and become wingless adult *Progredientes* (Fig. 13). These secrete much wax-wool and lay 20–30 brownish eggs, which give rise again to *Progrediens* and *Sistens* larvae: the latter hibernate in the first stage, the former, after two or perhaps three moults, develop to adult *Progredientes*, but no *Sexuparae* are produced from the first or any subsequent *Progrediens* generation. Throughout the summer and autumn, the *Progrediens* generations are continued until the time when the Larches lose their foliage.

Some of the *Progrediens* larvae produced from eggs laid by adult *Sistentes* were kept under observation in Hertfordshire in March and April, 1914, and developed as follows:

	Larvae found on Larch needle	First Moult	Second Moult	Third Moult	Adult oviposited
1.	March 16	March 25	March 29 (wax-wool secreted March 30)	April 2 (much wool secreted)	April 6–14
2.	„ 18	„ 26	March 31 (wool secreted April 1)	April 5	—
3.	„ 26	„ 30	—	—	—
4.	„ 29	?	April 6 (wool secreted April 8)	„ 14	—
5	„ 29	„ 31	April 2 (wool secreted April 4)	—	—
6.	„ 29	„ 30	April 2 (wool secreted April 4)	„ 8 (much wool secreted)	„ 9–14
7.	„ 29	„ 30	April 2 (wool secreted April 4)	April 8 (much wool secreted)	—
8.	„ 29	?	March 31 (wool secreted April 2)	April 4 (much wool secreted)	„ 6–14

The time from the hatching of the egg to the first moult is therefore

about ten days, the second stage lasts from 3–6 days, the third from 5–9 days, and oviposition about ten days.

The fact that wax-wool is secreted by third-stage larvae, two days after the second moult, may possibly have led Mr Steven to believe that only two moults altogether occur in the later *Progrediens* generations; at any rate, the matter is one of little importance, and can easily be cleared up.

III. STATISTICS OF THE COLONICI GENERATIONS.

A. SISTENTES.

The Sistens larvae all hibernate in the first stage, only becoming adult in the spring following; as found in nature, they have a triple origin:

(1) From eggs laid by the *Gallicola migrans*.

(2) From eggs laid by the first generation of Sistens derived from (1).

(3) From eggs laid by the Progredientes of several generations.

In February, 1914, adult Sistentes were observed on Larch in Hertfordshire, and the eggs laid by them collected, to determine the proportion of Progrediens and Sistens larvae hatching from them.

Eggs collected	Eggs hatched	Resulting larvae: Progrediens	Resulting larvae: Sistens
February 19	Feb. 27–March 6	66	0
,, 23	,, 26– ,, 7	60	0
,, 23	March 5– 7	18	0
March 12	,, 16–27	68	0
,,	,, 15–29	90	0
,,	,, 15–26	77	0
,,	,, 16–25	96	0
,,	,, 13–20	144	0
,,	,, 13–20	241	0
,,	,, 13–20	138	0
,,	,, 23–30	45	0
,, 18	April 4–10	76	0
Individual Eggs:			
February 14	February 26–28	6	0
,, 15	March 2–8	13	0
,, 19	,, 30–April 6	10	0
5 egg-clusters collected March 12	,, 12– ,, 10	524	0
	Total	1672	0

During these observations a few of the egg-clusters were kept in a warmed glass-house, the rest outside: in both cases there was a total

absence of Sistens larvae. It is noteworthy that Sexupara stages developed, though in small proportions, from these Progrediens larvae.

In May, 1919, the observations were repeated with egg-clusters obtained in the same locality.

Eggs collected	Eggs hatched	Progrediens larvae	Eggs hatched	Sistens larvae	Total
May 17	May 18–27	90	—	0	90
,,	,, 18–27	72	—	0	72
,,	,, 20–June 1	66	—	0	66
,,	,, 18–26	101	—	0	101
,,	,, 18–25	70	May 23–31	38	108
,,	,, 21–26	19	,, 18–31	139	158
,,	,, 21–25	7	,, 18–27	81	88
	Total	425		258	683

It is clear that variation exists from year to year in the proportion of Progrediens and Sistens eggs produced by the adult Sistentes. However, there seems to be some system in this variation.

First, a large proportion of the egg-clusters gave rise only to Progrediens larvae (all in 1914, 4 out of 7 in 1919). Secondly, some clusters produce a very large majority of Sistens larvae, in which case the eggs hatching first in the cluster were Sistens, and *not* Progrediens larvae.

Thirdly, in common with Mr Steven's observations, some clusters produce a majority of Progrediens, and a minority of Sistens larvae, in which case the first eggs hatching gave rise to Progrediens, and only the later ones to Sistens larvae.

As Mr Steven points out, observation extending over many years on isolated trees is necessary to determine with exactitude whether the Sistentes of the three origins produce constant proportions of the two forms, but the above statistics may well point to such research having a definite result, and perhaps even to the trend of that result.

B. Progredientes.

False proportions are easily obtained if egg-clusters, from which some of the larvae have already hatched and wandered away, are kept under observation.

From seven such clusters collected at Oxford on March 28th, 1914, 17 Progrediens and 25 Sistens larvae hatched between that date and May 18th. In June, 1913, five similar clusters produced 36 Progrediens, and 30 Sistens larvae, between June 14th and June 24th.

These represent the first Progrediens generation, in which the proportions seem to be fairly equal.

The late autumn generations were more closely studied in 1913 at Oxford, and the observations made show that differences of temperature, whether applied to the trees, to the individual insects, or to the eggs during oviposition, probably do not affect the resulting proportions of this generation, and certainly not to any appreciable extent.

Egg-clusters collected 1913	No. of eggs in cluster	Date of hatching 1913	Larvae resulting. Progrediens	Sistens	Conditions
October 19	15	October 22–27	6	4	Natural
November 12	10	November 12–20	9	0	Adult and eggs produced in warm temperature
,, ,,	18	,, 12–25	15	0	do. do.
,, 15	19	,, 19–24	11	4	Natural
,, ,,	15	,, 20–27	6	4	do.
,, 19	25	,, 23–29	25	0	Adult and eggs produced in warm temperature
,, 20	17	,, 24–29	15	0	do. do.
,, 30	28	December 4–10	28	0	Eggs brought into warm temperature after oviposition
,, ,,	22	,, 3–12	22	0	do. do.
,, ,,	26	,, 2–10	8	1 (Dec. 1)	do. do.
,, ,,	12	January 13–22, 1914	12	0	Natural (frost)
,, ,,	24	Nov. 30–Jan. 22, 1914	19	0	Oviposition in warm temperature. Eggs subjected to frost
December 4	5	December 10–12	4	0	Adult and eggs produced in warm temperature
,, ,,	4	,, 12–14	2	0	do. do.
		Total	182	13	

The great preponderance of larvae of the Progrediens type produced by the last generation of the year shows the assumption that only Sistentes hatch from the eggs to be completely false.

It may be noted that a continued exposure to a warm temperature causes a great diminution in the number of eggs laid, and, if climate plays any part at all, this seems to be the only direction in which any effect is produced.

Finally it is suggested that the sap-flow in the plant, and therefore nutrition of the insect in all stages, may well be a prominent determining feature in the production of Progredientes and Sistentes, in addition to the alternative generations from which they may primarily arise.

IV. ECONOMIC CONSIDERATIONS.

A diagram is here given representing every stage in the life-cycle of the Larch Chermes, and modified from that given by C. Börner in 1908, in order to show more accurately the origin and development of the Colonici generations.

The dotted circle in the Spruce cycle denotes the *Gallicola non-migrans* generation, and the Fundatrix generation arising from it, as described by Börner. These generations may occur in Germany, but in Great Britain we have no evidence that they exist, a fact which might modify the most economic means of control considerably.

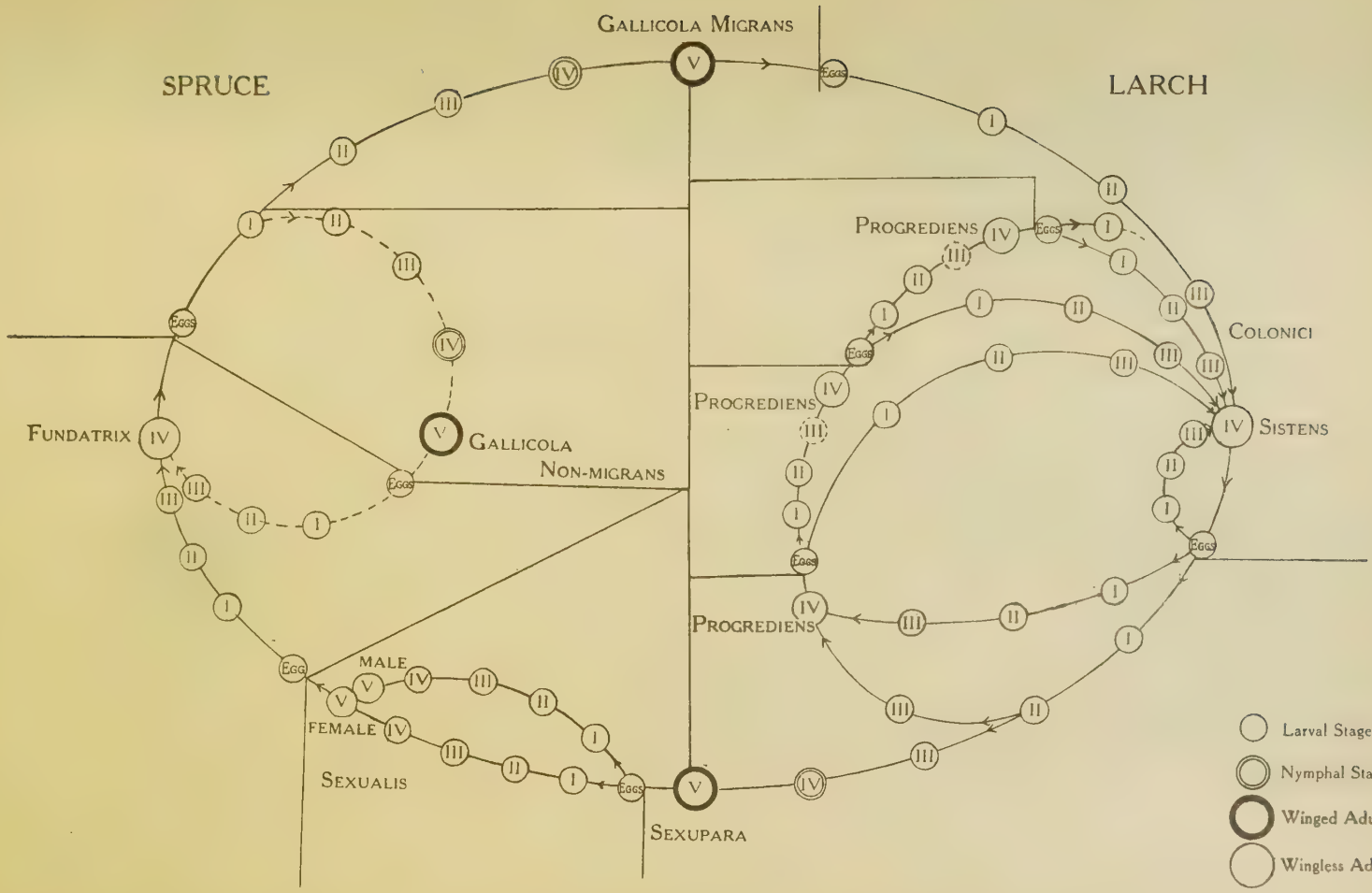
There is no doubt that the brunt of damage is sustained by the Larch in the case of young plants, and Mr Steven has shown that this can be adequately controlled by fumigation.

The Spruce does not appear to be attacked severely while young, and, as applied to Larch, it would certainly seem that a legislative measure is called for, providing for a compulsory fumigation of all Larch trees before planting out in the forest, not only upon the principle of starting with clean stock, but with a view to giving the individual plants a chance to make a good growth from the beginning.

With regard to older Larch trees, it is probable that a good control on the Spruce, growing in the neighbourhood, might well obviate the necessity of a costly and difficult control on Larch, for it now appears that a large majority of the Sistens larvae perish during hibernation, and there is no doubt that the Progrediens generations come to an end with the fall of the leaves, thus accentuating the benefit to be derived if the *Gallicolae migrantes* were prevented from their annual influx from the Spruce.

Except at unwarrantable cost, the galls on the Spruce could hardly be destroyed, and the wintering Fundatrix larvae, with their diffuse distribution over the Spruce buds, and their covering of wax-wool, would present many difficulties if spraying were resorted to. The Sexualis generation, however, is produced, by the Sexupara, on the underside only of the older Spruce needles, during a short period of the summer, and under the wings of the mother insect they remain during their development, only partially covered by an otherwise copious supply of wool, secreted by the parent.

It is the Sexual generation, then, about which least is known, that gives an opening for a method of control by spraying—a remedy rendered economic by the fact that only the underside of the branches need be


GALLICOLA MIGRANS
SPRUCE
LARCH
PROGREDIENS
COLONICI
PROGREDIENS
FUNDATRIX
GALLICOLA
NON-MIGRANS
SISTENS
PROGREDIENS
MALE
FEMALE
SEXUALIS
SEXUPARA
EGG
EGGS
Larval Stages
Nymphal Stage
Winged Adult
Wingless Adult

treated, and perhaps even more so, if it is found that the Sexuparae confine their oviposition only to the lower branches.

The principal economic investigation therefore still lies before us in a detailed study of the habits and structure of the Sexuales, and a determination of the presence or absence of the *Gallicola non-migrans* generation in this country.

Should the latter exist, it probably does so to a very limited degree, and the main control upon the Sexual phase would, in this event, be little disturbed.

V. A METHOD OF PREPARING APHIDAE FOR MICROSCOPIC EXAMINATION.

While investigating the life-history of the Larch Chermes in 1913, it was noticed that ordinary *Sulphuric Ether* had a peculiar effect in "fixing" the chitinous covering of the young stages of this insect, and so of preventing crinkling and distortion.

Later a use was found for this process in the preparation of more advanced stages, both winged and wingless, and in mounting Aphids of considerable size, in addition to insects of other Orders, having extremely delicate chitinous membranes.

Finally, for detailed examination, it was found possible, even with Aphids of considerable bulk, to subject the insects to pressure during Ether-fixation, the resulting *balsam* preparations showing a minimum of distortion, and presenting objects especially suitable for micro-photography.

Börner's method for preparing specimens of the Chermesidae in 1908 comprised a preliminary immersion in 70 per cent. Alcohol, and dehydration through 90 per cent. and Absolute Alcohol. The fats were then dissolved out in Sulphuric Ether, and the objects hydrated through Absolute, 90, 70, 50 and 30 per cent. Alcohols, with a final immersion in Distilled water. After clearing in weak Potash, and another immersion in Distilled water, Glycerine was added, and the skins finally mounted in a $\frac{2}{3}$ Glycerine solution.

Roughly this process takes the following time:

	Hours	Minutes
Preliminary Dehydration		15
Fat Dissolution	24	
Hydration		30
Clearing in Potash	6	
Mounting in Glycerine		15
Total	31	

In addition, Borner found it necessary to open the bodies of the larger forms before preparation, so that the method is very long, and glycerine preparations are neither permanent nor very satisfactory.

For quicker, more permanent, and equally satisfactory mounting, the living insect is placed on a glass slide and a cover-glass (large for large objects) is placed over it. A few drops of *Sulphuric Ether* are run beneath the cover-glass, and the ether allowed to evaporate until the pressure of the cover-glass forces out a portion of the contents of the insect; their escape takes place through minute interstices in the chitin of the head, and extremity of the abdomen. For large objects, it is necessary to add a little pressure by means of a needle. The slide is then flooded with Absolute Alcohol, and the cover-glass removed with a fine needle, carefully.

In the majority of cases the object sticks either to the slide or cover-glass, and if sufficiently cleared, as is often the case with small insects, may be mounted in balsam, as described below. The time taken by this process does not exceed 5 minutes.

If, however, clearing with Potash is demanded, the object, after the above treatment with ether and absolute alcohol under the cover-slide, is first hydrated, through the alcohols, into distilled water, cleared in 2 per cent. Potash Solution, and again dehydrated through distilled water to Absolute Alcohol. To the latter, drops of *Turpineol* are added slowly, and finally the object, after immersion in pure Turpineol, is mounted in Canada Balsam (Xylol Solution).

The time taken over this method is roughly as follows:

	Hours	Minutes
Ether-fixation and Hydration		20
Clearing in 2 per cent. Potash Solution	3	
Dehydration		20
Final Clearing in Turpineol and Mounting		5
Total	3	45

The objects, after treatment with ether, are flat, and therefore require considerably less time in dehydration, hydration, and clearing with potash, than in Börner's method.

The final clearing reagents, Clove Oil and Xylol, are unsuitable for these preparations, as distortion and contraction are liable to result, especially after the use of potash. These inconveniences are readily surmounted in their substitution by Turpineol. Chitin-stains, such as "orange," are strongly deprecated.

A number of insects may be treated with the ether on the same

slide, and then transferred through Alcohol absolute and 90 per cent. to Alcohol 70 per cent. If any stick to the slide or cover-glass they may be gently removed with a needle, and kept in the Alcohol until time for complete clearing and mounting is available.

It is, however, not advisable, though it is quite possible, to mount more than one specimen under one cover-glass.

The moulted skins of Aphids and other insects lend themselves especially to this mode of preparation, which is justified by the fact that no less than five pairs of delicate glands, not previously described as constant, have made themselves, and the number of their facets, apparent upon the ventral side of the Progrediens larva of the Larch Chermes, immediately after hatching from the egg.

From measurements taken, it would seem that the expansion produced by the pressure on the organism during the process is just compensated for by the contraction which takes place subsequently in dehydration and in the approximation of the dorsal and ventral surfaces, or of the sides, and the insects can be prepared in any position required. Material which has first been preserved in alcohol cannot, of course, be subjected to this process.

The following photographs, except where indicated in one case, have been taken directly from these preparations, and illustrate the stages of the Colonici sistens and progrediens, and the Sexupara, on Larch (*Larix europaea*).

EXPLANATION OF PLATES VI AND VII.

Cnaphalodes strobilobius, Kalt.

Development of Colonici and Sexupara on Larch.

Photographs direct from Preparations. × 50.

Fig. 1. Sistens. Stage I. Before hibernation.
„ 2. „ „ I. After hibernation.
„ 3. „ „ II.
„ 4. „ „ III.
„ 5. „ „ III. Moulted skin.
„ 6. „ „ IV. Adult.
„ 7. Progrediens. Stage I.
„ 8. „ „ II. Moulted skin.
„ 9. Sexupara. Stage III. Moulted skin.
„ 10. „ „ IV. Nymph.
„ 11. „ „ V. Adult.
„ 12. Progrediens. Stage III.
„ 13. „ „ IV. Adult.

Fig. 1. Potash-glycerine preparation.

Figs. 2–13. Ether-potash-balsam preparations.

Figs. 1–7, 10, 11, and 13 from photographs taken by Messrs W. Watson and Sons, 313 High Holborn, London.

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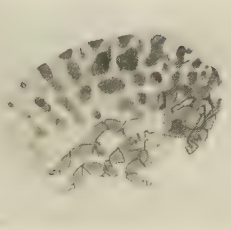

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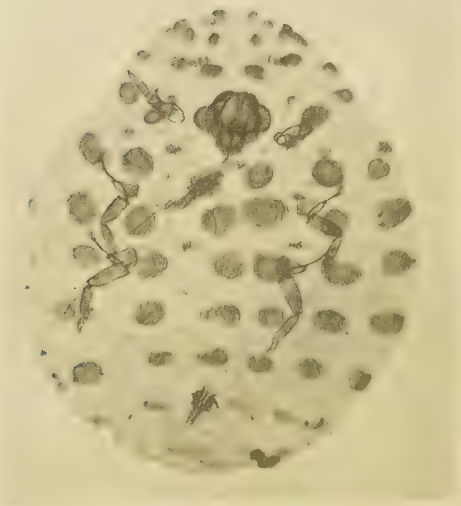

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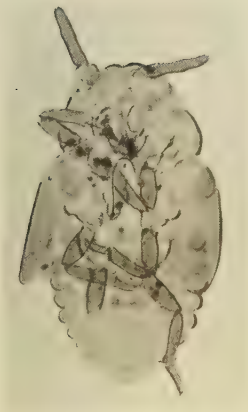

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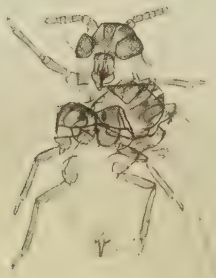

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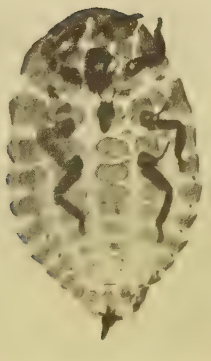

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STUDIES IN BACTERIOSIS. IV.—"STRIPE" DISEASE OF TOMATO.

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(With 5 Text-figures and Plates VIII and IX.)

INTRODUCTION.

The disease of tomatoes known to the nurseryman as "Stripe" is characterised by brown longitudinal markings or stripes on the stem, by shrivelling of the leaves, and by sunken irregularly shaped pits usually of a brown colour on the fruit. It is a specific communicable disease due to a bacillus which has previously been described as the cause of a very similar disease of the sweet pea.

So far little is known concerning the geographical distribution of the disease. It is very common on tomatoes grown under glass in this country and in the Channel Islands. There is no doubt that it occurs also in parts of Canada and the United States. Howitt and Stone(2) have given a description of a tomato disease occurring in Ontario and Pennsylvania, which agrees exactly with that here described. These workers, however, failed to obtain any causal organism and believe their disease to be due to some chemical or physical deficiency in the soil. Bailey(1) in 1892 and Selby(7) in 1897 both seem to have had this disease before them.

In many cases the disease is not of a very serious nature, by most nurserymen it is regarded rather as a nuisance than as a disastrous pest for, with care, a moderate crop of fruit can be obtained from plants which have been attacked. At times, however, the disease may be so prevalent as to ruin the whole crop.

INCIDENCE OF THE DISEASE.

Sometimes, during the first years of a nursery, plants have shown a considerable amount of disease, but this has gradually diminished until only a small percentage of the plants have been attacked in the later years. Conversely, cases are known where "Stripe" has appeared and gradually increased after some ten or twelve years during which time no sign of the disease has been observed. These facts would seem to indicate the soil as the main source of infection and Howitt and Stone (2) have shown that plants grown in soil from an infected house developed the disease while plants grown in the same soil previously sterilised remained free. The disease may appear in the seed-boxes, producing rapid destruction of the young plants and compelling fresh sowings to be made; it is not uncommon to find the first symptoms of disease while the young plants are still in the small pots (sixties) or again after these have been planted out in the houses for a fortnight or so. Usually, however, the disease first appears about May, when the earliest fruit is ready for picking, but frequently no signs appear until the tops are allowed to develop, when these often become badly attacked.

There is a distinct connection between soft and rapid growth and the incidence of disease, plants growing rapidly in the early stages are more liable to "Stripe" than others of a hardier nature. In one case observed at Cheshunt the plants were so badly attacked that it seemed impossible for the crop to recover, the conditions were then altered so as to induce a slower rate of growth with the result that the plants completely "grew out of" the "striped" condition, showed perfectly clean tops and yielded a good crop of sound fruit.

OBSERVATIONS ON THE EXPERIMENTAL PLOTS.

During the past season observations have been made on the manurial plots in the houses at Cheshunt to ascertain the relation of manurial treatment to the incidence of the disease. The indications are that a soft rapid growth such as is produced by excess of nitrogen and a high temperature accompanied by damping renders the plant more susceptible to stripe than does a hard slow growth accompanied by suitable additions of potash.

These observations are fully confirmed by inoculation tests carried out on plants grown in pots, the results of which will be found under the heading "Inoculation Experiments."

The effect of different manurial treatments on the incidence of stripe.

Variety	Treatment	Total No. of plants	No. of diseased plants
Comet	*C.A. without potash	120	78
,,	Control untreated	120	50
,,	C.A. with dung	120	45
,,	C.A. without Phosphates	120	41
,,	C.A.	120	40
,,	C.A. without nitrogen	120	34
,,	Double C.A.	120	34
Kondine Red	C.A. without potash	120	33
,,	C.A. with dung	120	33
,,	Control untreated	120	30
,,	C.A. without phosphates	120	28
,,	C.A. without nitrogen	120	19
,,	Double C.A.	120	14
,,	C.A.	120	13

* C.A. = complete artificials.

The effect of "damping" on the incidence of the disease.

	Damped		Not damped	
Variety	Total plants	No. striped	Total plants	No. striped
Comet	260	124	260	110
Fillbasket	260	112	260	95
Kondine Red	260	112	260	82
Ailsa Craig	260	95	260	34

The effect of forced and slow growth on the incidence of the disease.

	Forced growth		Slow growth	
Variety	Total No. of plants	No. of diseased plants	Total No. of plants	No. of diseased plants
Fillbasket	100	58	100	44
Comet	100	38	100	26
Kondine Red	100	24	100	14
Ailsa Craig	100	24	100	16

Besides showing the effect of manurial treatment and of forcing conditions these tables bring out clearly marked differences in the relative susceptibility of the varieties tested and point to the selection or breeding of a resistant variety as one means of controlling the disease.

THE MODE OF INFECTION.

As stated above the most usual mode of infection would appear to take place underground; young attacked plants show on examination a

brown discoloration of the root cortex (Fig. 1). The frequent occurrence of disease in the seed-bed suggests that the seed from infected fruit may also be infected or carry the causal organism externally though so far no actual proof of this has been obtained. Observations in nurseries and practical experiments have shown that the disease may sometimes spread downwards; successful "prick" inoculations have been made on

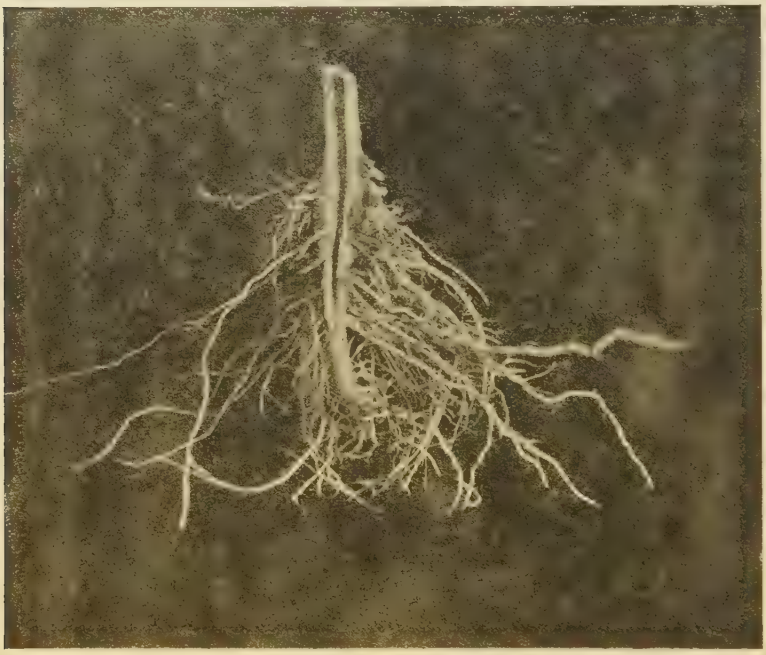

Fig. 1. Showing brown stripe on the root of a tomato plant affected with "Stripe Disease."

the upper parts of plants and indicate that insects may produce infection of these parts. It is also fairly certain that the pruning knife is a potent factor in spreading the disease; in one house it was observed that disease had spread from one end on both sides of the house while in another it had spread a certain distance down one side only, in the former case it was shown that the pruning had been across the house from left to right, while in the latter the pruning had been down one side and up the other.

SYMPTOMS OF THE DISEASE.

The stem of an attacked plant shows the earliest symptoms of disease as light or dark brown to black sunken patches of irregular shape, varying from small spots to long furrows and "blazes"; the blazes are often three or more inches long and frequently extend over the entire length of an internode. They are well shown in the photograph, Plate IX, fig. 1. In slight cases these markings occur intermittently along the stem while in bad cases the typical furrows can be found throughout the whole length of the stem and on the leaf and truss stalks. The name "Stripe" aptly describes this distinctive feature of the disease, but it

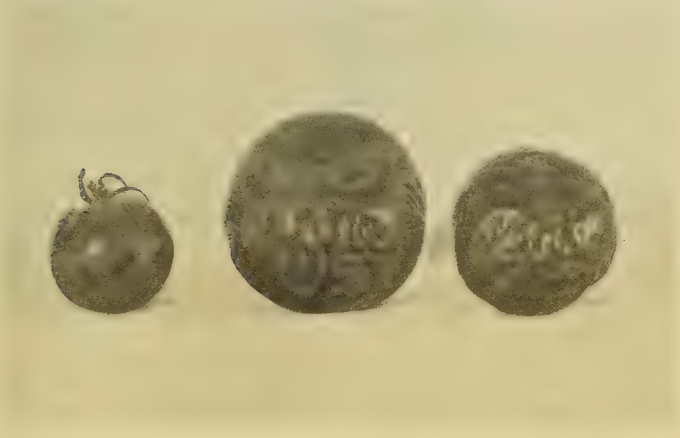

Fig. 2. Showing ripe fruits of tomato infected with "Stripe Disease."

should not be confused with the "Black Stripe" supposed to be due to *Macrosporium solani*[1].

On the leaf the disease first appears as yellow blotches near the mid-rib and the main veins. These later turn brown and extend so that finally the greater part of the surface becomes browned and much distorted by the shrivelling of the diseased areas.

The fruits show light or dark brown sunken patches with round or irregular outline well shown in Figure 2, Plate VIII and Plate IX, figs. 4

[1] There is however considerable doubt whether this is a distinct disease. It seems highly probable that *Macrosporium solani* exists as a saprophyte upon the tissue destroyed by the "Stripe" bacillus. This is emphasised by the fact that W. Dyke (quoted by "W" in *Gard. Chron.* 51, p. 52, 1912) thought that this fungus was the cause of Streak Disease of Sweet Peas, a disease now known to be due to a bacillus.

and 5. They vary from a few spots developed near the calyx to many scattered promiscuously over the surface of the fruit. They greatly reduce the market value and in bad cases, as in Plate VIII, the fruit is rendered quite unsaleable, being almost covered with these pock-like depressions.

Attacked plants become very brittle and are easily broken by the workers. In the worst case the whole plant becomes covered with lesions and finally dies.

MORBID ANATOMY.

Lesions in the pith and cortex are the characteristic internal features of the disease, the walls of the attacked tissues are strongly browned so that the patches are readily seen on splitting the stem with a knife. Plate IX, fig. 2 shows rather advanced lesions in the pith of a stem and fig. 1 shows a typical lesion in the cut petiole. In older stems which have become hollow, small brown patches occur in the remains of the pith and in the cortex but at the nodes where the pith is close and moist the patches are much larger. Microscopic examination of the stem seldom reveals the presence of the parasite in a living condition in these patches, but the walls stain deeply with fuchsin and the intercellular spaces are choked with deeply staining material strongly indicating bacterial attack. The appearance of the diseased tissue is not that of a soft rot though the middle lamella is partially destroyed. The cells appear to be torn asunder by shrinkage of the dead cells and tension set up by growth of the surrounding healthy tissue (see Fig. 3): eventually large cavities are produced in this way.

The roots are often found to be diseased only in the upper portion and infection can usually be traced to some wound or insect puncture just below the ground level; the tissues of the lower roots are in these cases white and apparently healthy. In some cases, however, no wound can be discovered, but the cortex is found to be browned to a considerable depth below the soil level and microscopic examination shows the presence of the bacillus in the tissue. It seems that penetration of the root may occur without the aid of a wound, but of course there is always the possibility that a small wound has escaped observation or again that the disease has spread down to the root from an aerial infection.

From the root the organism travels up the stem in the peripheral parts of the pith next to the proto-xylem elements. The organism is very seldom found within the wood vessels themselves, and for some considerable time despite careful examination one could not demonstrate the

A tomato plant badly attacked with Stripe Disease.

passage of the organism through the vascular cylinder to the cortex, where it produces the typical lesions or external stripes. Ultimately,

Fig. 3. Transverse section of a Striped stem through the browned region of the cortex. The black masses indicate the attacked cell-walls which harbour the bacteria. *A*. The distorted cells of the collenchyma. A_1. Collenchyma cells showing the destruction of the middle lamella. *C*. Healthy cortex cells. *D*. Attacked cortex cells.

however, the process was made clear by a series of transverse and longitudinal sections. The bacilli work outwards towards the parenchymatous elements of the wood or the medullary rays, the cell-walls

become swollen and browned, and the middle lamella is destroyed, thus opening up a passage for the organism (see Fig. 4). The wood parenchyma is distorted and browned and occasionally the wood vessels themselves are attacked and their walls disintegrated. Once through the vascular region the organism readily finds its way through the cortex to the exterior where it spreads upwards in the outer cortical layers and epidermis; the affected cortical cells collapse and the characteristic depressed stripe is thus produced on the surface of the stem. Anatomical examination of artificially infected plants has fully confirmed the conclusions drawn from naturally infected stems.

ISOLATION OF THE CAUSAL ORGANISM[1].

The organism was first isolated in September, 1918, from plants grown under glass without artificial heat. The plants were badly attacked when first observed and the crop of that house was an entire failure. Sections of the stems showed no sign of active bacteria and several attempts to isolate the organism from the stem proved abortive. In one instance out of perhaps twenty attempts a yellow organism in company with others was obtained on plating from the diseased pith and this afterwards proved identical with an organism which was much more readily obtained from diseased patches on the fruits. Many of these fruit spots seemed to be sterile and frequently on incubation of a diseased fruit the disease failed to extend further. It must be concluded that the organism which had given rise to these diseased patches was no longer viable. A similar case of the disappearance of a plant parasite in diseased tissue has been briefly described in the disease named by one of us (Paine (5)), the Internal Disease of the Potato, and has been suspected by the same author in a Leaf Spot Disease of *Protea* (6). It is quite probable that *bacteriolysis* in plant tissues is a more common phenomenon than it is at present believed to be. This may account for the fact that Howitt and Stone (2) and the four well-known bacteriologists to whom they submitted diseased plants failed to isolate any causal organism from tomatoes bearing exactly the same symptoms as are associated with our "Stripe."

The organism can often be seen in the intercellular spaces of sections of diseased tissue from a fruit spot, and platings made from such tissue

[1] The joint authors of this paper isolated the same organism independently and finding they were studying the same disease agreed to collaborate. The cultural work has been carried out by the first-named author at the Imperial College, while the other is responsible for the inoculation experiments which have been conducted at Cheshunt.

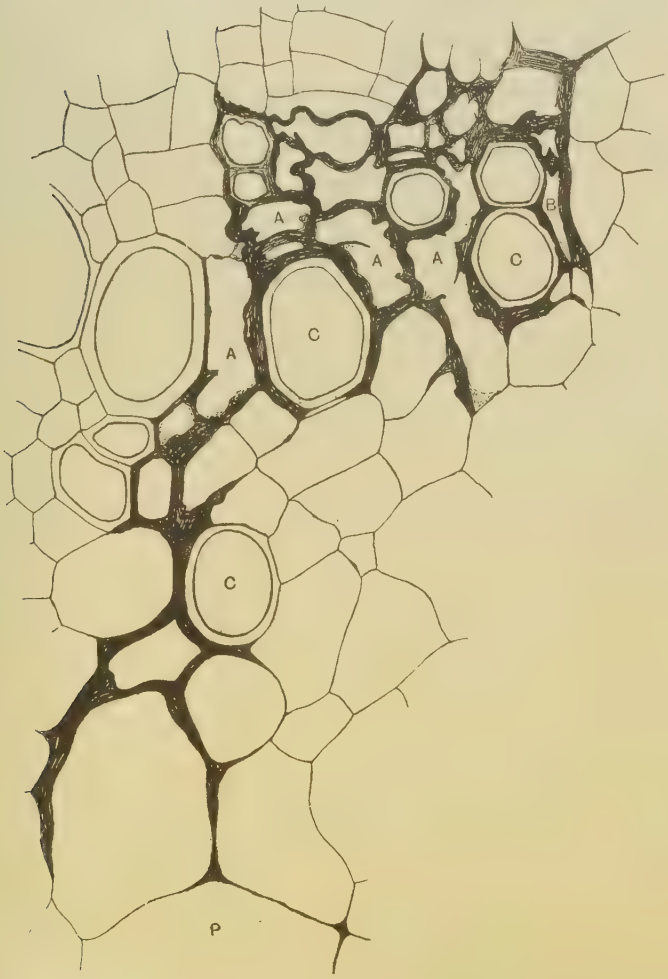

Fig. 4. Transverse section through the vascular bundle showing the passage of the organism from the cortex to the pith. *A*. The wood parenchymatous cells undergoing disintegration by the organism. *B*. Cavity left by the destruction of the middle lamella. *C*. Wood vessels. *P*. Pith.

have often yielded pure cultures without difficulty. On two occasions, from a fruit and a stem respectively a distinctly different organism was found in great preponderance and in fact in almost pure condition. This organism caused no disease when inoculated into plants; it is briefly described below since it agrees in all its characters with *Aplanobacter michiganense*, which has been described by Smith(8) as the cause of a disease in tomatoes.

DESCRIPTION OF THE CAUSAL ORGANISM.

A. Morphological Characters.

The organism is a small yellow oval rod measuring from 1·2μ to 2·0μ in length and 0·8μ to 1·0μ in width; pairs are not common but are found up to 3·4μ in length. These measurements were made on a preparation from a broth culture incubated 24 hours at 22° C. fixed in formalin and stained with aqueous methyl violet.

It is a motile organism with peritrichous flagella usually from four to six in number and from four to ten micra in length. The flagella stain well by the method of van Ermengem (see Fig. 5). The organism rapidly comes to rest when grown on solid media, sometimes within 24 hours, but remains motile for three or four weeks in broth cultures. Examined in water suspension under a cover-glass the motion is of the "free swimming" type with frequent spells of "tumbling" on the short axis. At the centre of the cover-glass the motion slows down considerably after half-an-hour, but continues for upwards of three-quarters of an hour to one hour.

Staining capacity. The bacillus stains readily with carbol fuchsin, Victoria blue and methyl violet. It is gram negative.

Capsules. The presence of a capsule has been suspected round organisms forming a ring at the surface of broth cultures and in cultures in Uschinsky solution. They could not be seen under dark-ground illumination and it has not been possible to demonstrate them by staining. Films from Uschinsky solution stained with gentian violet frequently show a clear halo around each organism and the distribution of the organisms in a crowded film is what one would expect for a capsulated organism, *i.e.* the stained rods are never actually in contact with one another. If a capsule is present it is not a very wide one and does not stain by the usual methods employed for capsule staining.

B. Cultural Characters.

In all cases, unless otherwise stated, the incubation temperature has been 22° C.

Plate cultures in bouillon agar + 10. The colonies on poured plates show after 24 hours; surface colonies have a diameter of $\frac{1}{2}$ to 1 mm., depth colonies are lenticular and just visible with a lens. The surface colonies are round, raised, wet-shining, with a tendency to excentric development from a depth colony. The colour is a mid-chrome by reflected and somewhat milky by transmitted light.

Fig. 5. Showing *Bacillus lathyri* stained by Steven's modification of van Ermengem's method.

Streak cultures on bouillon agar + 10. The streak is raised, wet-shining, butyrous yellow, with entire margin.

Stab cultures on bouillon agar + 10. Growth is visible along the stab after two days as a narrow yellow streak right to the bottom of the stab. The margin is slightly echinate. The surface colony after five days has a diameter of 4 mm. and a bright yellow butyrous appearance.

Plate cultures on bouillon-gelatine + 10. Colonies appear on the second day, are 2 or 3 mm. in diameter on the third day, and show no sign of liquefaction for 8–10 days. A liquid halo then appears and

eventually after some three weeks a liquid basin is formed with a yellow granular precipitate at the bottom.

Stab culture on bouillon-gelatine + 10. Growth was visible after 48 hours. On the third day there was no liquefaction, the margin of the stab was echinate and that of the surface colony smooth and round. There was still no liquefaction on the seventh day. The tubes were then taken from the incubator and when examined a fortnight later liquefaction had commenced at the top. Liquefaction was very slowly produced and even after six weeks only the upper portion of the stab had become saccate. A granular yellow precipitate had collected at the bottom of the liquid portion.

Cultivation on other media. The organism grows well on media of many plant extracts. Especially well on potato-mush-agar, on "Marmite" (yeast extract) agar and in milk. Good growth was also obtained on cabbage and celery agar. The most favourable reaction appears to be about + 5 of Fuller's scale. The limits of tolerance towards alkali were not determined.

Streak culture on cooked potato. Growth was apparent after 24 hours. On the second day the streak was 3 mm. wide, bright yellow, raised and butyrous. No stain was produced in the surrounding potato tissue.

Thermal death point. Tubes of bouillon were immersed in a thermostat at 45°, 47°, 49°, 51°, 53°, and 55° C. The hot broth was inoculated with a loopful of a bouillon culture 24 hours old and left in the bath for 10 minutes at each temperature. On subsequent incubation those heated above 51° C. failed to become turbid.

C. Physiological Characters.

For the following tests a 48-hours agar culture was used to inoculate the tubes and the incubation temperature was 22° C. The strains isolated independently by the two authors were set up in parallel and always produced identical results.

10 *per cent. peptone* + 2 *per cent. glucose.* The colour of the litmus became faintly red on the second day, a ring had formed and a loose pellicle, but no gas. On the seventh day the acidity was not much more marked, the colour was slightly redder than the control, no pellicle formed but a decided ring; a very small bubble of gas had collected in the Durham's tube, it had not a greater volume than that occupied by the head of a match and later became almost entirely dissolved. The colour remained practically of a neutral tint for some time and finally

only brown. On titration after two months' incubation the original 10 cc. required 1·3 cc. of $\frac{N}{10}$. NaOH for neutralisation against phenolphthalein as against 1·0 cc. required by the control. This small degree of acidity and small development of gas were consistently observed but they do not appear to justify the classification of the organism as a glucose fermenter. They possibly arose from some impurity in the sample of peptone employed although a control tube of peptone without sugar did not give this result. The organism was still motile in the brown broth when examined after 26 days.

10 *per cent. peptone* + 2 *per cent. lactose.* The colour remained neutral. A strong ring formed but no pellicle.

10 *per cent. peptone* + 2 *per cent. sucrose.* Precisely the same as in case of glucose above.

Bouillon + 2 *per cent. mannite.* Became acid on the fifth day. No gas formed.

Bouillon + 1 *per cent. nitrate.* Slightly turbid on the first day and nitrite was present. On the second day the nitrite was strongly positive and remained so for two months. Turbidity was never very strong, no ring or pellicle was produced but the broth became somewhat mucoid.

Potato plug. About 1 cc. volume of the plug taken from half-way down ground in 200 cc. of water on addition of 1 cc. of iodine gave a bright red colour, no trace of starch remained. Diastatic action is therefore strong.

Uschinsky solution. Distinctly turbid on the second day, a ring had formed and the colour was neutral. On the fifth day the litmus had begun to bleach, a strong yellow ring had formed and a loose pellicle which was easily broken up. After twenty days the litmus had become completely bleached, a strong yellow ring and pellicle were formed and a large yellow deposit filled the lower half of the tube. This was very mucus-like and spread on a slide almost like a sputum. As stated above capsules were suspected to be present, especially in the yellow ring, although no demonstration of a capsule could be obtained.

Dunham's solution. Became turbid on the second day, a loose yellow pellicle formed later. Indol was tested for on the thirteenth day but was not present.

RELATIONSHIP OF THE CAUSAL ORGANISM.

Comparison of the above characters with those of other plant parasites leads to the conclusion that the organism here described is closely related to, if not identical with, *Bacillus lathyri* found by Manns and Taubenhaus (4) as the cause of diseases of the sweet pea, red clover and soya bean, etc. A full description of this organism published by Manns (3) shows close agreement with the above. Noteworthy points of similarity are: (1) the morphology; the position of the flagella being rather unusual for a bacillus, they are certainly peritrichous but there is a marked tendency for those at the anterior end to be lacking in stained preparations (see Fig. 5): (2) the butyrous and viscid growth on most solid media; (3) the mucoid development in fluid media, especially in Uschinsky solution; (4) the slow liquefaction of gelatine; (5) the effect in litmus milk. Only two points of difference appear: (1) in the resistance to heat; *B. lathyri* has a thermal death point of 48° C. and shows no growth at 37½° C. whereas the "Stripe" organism has a thermal death point of 51° C. and does grow, though very sparingly, at 37—38° C. It is quite conceivable that continued existence at the temperature of the forcing house may have raised the heat-resisting power of the strain; (2) in the power to reduce nitrates; Manns found no reduction of nitrate by *B. lathyri* though in this connection he states "Several of the strains produce nitrites from peptone broth; thus in nitrate broth unless quantitative determination is made for the nitrates placed therein one might easily assume nitrate reduction." Special care was therefore exercised in determining the reducing power of the "Stripe" organism. Pure strains from three separate isolations of the organism were inoculated each into six tubes of beef extract ("Jardox") with, and six tubes without, the addition of 1 per cent. potassium nitrate. After incubation for three days all the eighteen tubes containing nitrate gave positive reactions for nitrite while the eighteen controls without nitrate gave negative results. Nitrite was shown by azo-colour formation in the sulphanilic acid + α naphthylamine reagent. This is a very delicate test for the presence of nitrite and is probably more reliable than the method of determination of nitrate adopted by Manns.

The crucial test of identity will be the cross-inoculability of the "Stripe" organism from the tomato to the sweet pea[1]. This has not

[1] In this connection it is noteworthy that Manns has isolated *B. lathyri* from tomatoes showing Blossom-End Rot and has been able to produce the symptoms of this disease by artificial infection of tomatoes with a strain of *B. lathyri* isolated from a species of *Lathyrus*.

been attempted as yet for the reason that the identity of the organism with *B. lathyri* was only discovered after this paper had been sent to the press. Experiments to settle this point will be made next summer.

INOCULATION EXPERIMENTS.

Preliminary Experiments.

28. 5. 19. Six young tomato plants (Comet variety) were used. The stems were washed with alcohol and then with sterile water. A small piece of culture was pricked in near the top of the plant and the wound covered with tin-foil to avoid secondary infection.

31. 5. 19. Brown corky patches appeared round the stab.

11. 6. 19. Black furrows up and down the stem from the stab. Three inches up and two down.

28. 6. 19. Typical black furrows on the stem up and down from the wound. Leaves browned in patches. General appearance of striped plants.

Three controls were perfectly healthy.

28. 5. 19. Six young plants as in the previous experiment were used. Inoculations were made by pricking in a piece of culture near the base of the plant and covering as before.

14. 6. 19. Black furrows eight inches up the stem. Lower pair of leaves attacked.

30. 6. 19. Plants smothered in lesions.

Three controls were perfectly healthy.

28. 5. 19. Six plants removed from the soil and their roots well washed. They were then washed in alcohol followed by sterile water. They were inoculated by rubbing a piece of culture on the roots, and were then re-planted.

15. 6. 19. First brown patch appeared on the stem about half an inch above the soil level.

29. 6. 19. Lesions on the stem seven inches from the ground.

5. 7. 19. Plants badly attacked.

Three controls quite healthy.

5 7. 19. Organism re-isolated from representative members of each experiment.

3. 6. 19. Four plants two feet high were inoculated by rubbing a piece of culture on a rough leaf-base such as is left by careless pruning.

8. 6. 19. Bases blackened and furrows appear which run from the base to the stem.

15. 6. 19. Furrows down the stem two inches below the inoculated base.

3. 7. 19. Furrows up and down the stem. First and second pair of leaves above and the first pair below the point of inoculation attacked. Two controls healthy.

3. 6. 19. Four plants two feet high were used. Several badly striped leaves were crushed in a mortar and the juice rubbed into a carelessly pruned leaf-base.

11. 6. 19. Bases blackened.

30. 6. 19. Typical stripe furrows running from the bases into the stem were visible.

21. 7. 19. The plants were all badly striped.

Four controls made by rubbing the juice of healthy leaves into jagged leaf-bases were perfectly healthy.

3. 6. 19. Four green tomato fruits were inoculated by pricking in a small piece of culture after sterilising the outside.

10. 6. 19. Brown ring round the prick.

17. 6. 19. Brown sunken patch round the prick. The fruit was cut open when it was found that the tissue round the stab was browned. A brown patch was present in the loculus wall, from which the organism was re-isolated.

The control fruit showed the wound healed and no sign of stripe.

20. 7. 19. The organism re-isolated from inoculated plant on 5. 7. 19 was pricked into six twelve inch plants.

29. 7. 19. Typical furrows on stem near the wound.

4. 8. 19. The organism was again isolated and found to be identical with the original.

The effect of manuring upon the results of artificial infection.

A standard soil compost was made up as follows:

72 cubic feet of virgin soil,
32 lbs. lime,
8 „ bone meal,
8 „ bone flour.

72 twelve inch pots were each given one cubic foot of the compost. To these pots nitrogen in the form of ground hoofs and potash as sulphate of potash were added in varying amounts. Each series consisted of eight pots planted with uniform tomato plants of the variety Comet.

Series 1.	1 c. ft. compost and	$\frac{1}{9}$ lb. hoofs per pot			
„ 2.	1 „ „	$\frac{2}{9}$ „ „ „			No potash
„ 3.	1 „ „	$\frac{3}{9}$ „ „ „			
„ 4.	1 „ „	$\frac{1}{9}$ „ K_2SO_4 „			
„ 5.	1 „ „	$\frac{2}{9}$ „ „ „			No nitrogen
„ 6.	1 „ „	$\frac{3}{9}$ „ „ „			
„ 7.	1 „ „	$\frac{1}{9}$ „ hoofs and $\frac{1}{9}$ lb. K_2SO_4 per pot			
„ 8.	1 „ „	$\frac{2}{9}$ „ „ „	$\frac{2}{9}$ „ „	„	Complete
„ 9.	1 „ „	$\frac{3}{9}$ „ „ „	$\frac{3}{9}$ „ „	„	

28. 5. 19. Six plants of each series were inoculated by "pricking in" some of the culture into the lower portion of the stem and covering the wound with a piece of tin-foil to prevent secondary infection. Two plants of each series were left as controls. They were pricked with a sterile needle and covered in the usual way.

Series 1.

31. 5. 19. Brown corky appearance round the stab.

12. 6. 19. First pair of leaves above the wound showed typical stripe lesions. Furrows three inches up the stem.

20. 6. 19. Plant typically striped two feet up the stem.

Series 2.

31. 5. 19. Lesions round the "prick" more distinct than in Series 1.

12. 6. 19. Furrows nine inches up the stem.

20. 6. 19. Lesions more advanced than in Series 1.

Series 3.

31. 5. 19. Discoloration still more intense than in Series 2.

12. 6. 19. Furrows up the stem eleven inches.

20. 6. 19. Five out of the six plants showed lesions in the tops. The sixth one had the top seven inches clean.

Series 4.

31. 5. 19. Slight discoloration round the "prick."

12. 6. 19. Furrows two inches up the stem from the wound.

20. 6. 19. Very little stripe on four plants, but two showed lesions on the first pair of leaves above the wound.

Series 5.

20. 6. 19. Very little stripe showing on any plant.

Series 6.

No stripe at all, except in one case where the plant had rooted through the pot into the rich soil beneath.

Series 7.

Similar appearance to plants in Series 1.

Series 8.

Similar to Series 1.

Series 9.

12. 6. 19. Like Series 2. Furrows up to three inches above the wound.

20. 6. 19. Third pair of leaves above the wound attacked.
All controls healthy.

21. 8. 19. The preceding experiment was repeated with precisely the same results. The indications were that increasing amounts of nitrogen without potash produced an increasing susceptibility to the disease, while increasing amounts of potash without nitrogen gave a corresponding increase in resistance to it. Where potash and nitrogen were used together there were indications that the potash counteracted the effect of the nitrogen.

CONTROL OF THE DISEASE.

Several methods are suggested:

(1) Sterilisation of the soil by heat.

(2) Sterilisation of the seed by means of formaline.

(3) Selection of resistant varieties.

(4) Sterilisation of the pruning knife in cases where the disease has been noticed, especially while pruning the diseased plant and before passing from the diseased plant to healthy ones. This might easily be effected by wiping the blade of the knife with a rag soaked in 2 per cent. lysol or some similar disinfectant. The prunings from diseased plants should not be thrown to the ground but carefully collected and burnt.

(5) The cutting away of a diseased stem and allowing a lateral to develop will often give a clean plant.

(6) Care in the use of artificials to see that potash is present in sufficient quantity and nitrogen not inordinately abundant.

COMPARISON OF THE STRIPE DISEASE WITH THE GRAND RAPIDS TOMATO DISEASE.

The Grand Rapids Disease has been investigated by Smith(8) and attributed to a bacterium which he has named *Aplanobacter michiganense*. It has been stated earlier that an organism was isolated from "Striped" plants which seems to agree closely with *A. michiganense*. The organism is a small oval non-motile rod, gram positive, growing well on neutral or slightly acid media forming a very viscid, deep orange-coloured slime, so viscid in fact that, when the culture is young, difficulty is experienced in lifting any of the slime on a platinum wire. In old cultures this difficulty is not so great. The colour of litmus milk remains unchanged for 10 days to 14 days at 22° C. and a thick deep yellow mucilaginous ring and pellicle form at the surface, the casein is not coagulated but becomes slowly digested; at the end of a month the whey is quite clear and red, and a precipitate containing tyrosine crystals is found at the bottom of the tube. In untinted milk the yellow ring is again the only noticeable change during the first fortnight, after which the casein is digested slowly without coagulation and the whey becomes quite clear and bright yellow in colour. Nitrates are not reduced, slight turbidity is formed in the nitrate broth but no ring or pellicle is produced, in three days at 22° C. the broth becomes very mucus-like and the organism is found in short chains appearing almost like a *streptococcus*, except that the component cells are oval in shape. Dunham's solution became slightly turbid and mucus-like, indol was produced.

No growth was observed in 10 per cent. peptone containing 2 per cent. of glucose, lactose or saccharose and the colour of the litmus remained unchanged even after a month in the incubator. No growth was obtained in Uschinsky solution.

A comparison of these reactions with those described by Smith for

Aplanobacter michiganense make it at least probable that the two organisms are identical. But whereas Smith claims to have made repeated successful inoculations with his organism and has stated that virulence is retained for some months in artificial cultures the organism here described has not shown any sign of parasitism, although repeated attempts at infection have been made, the earliest being within 10 days of its isolation from the plant.

Three possibilities then arise. Firstly, the strong similarity between *A. michiganense* and the organism here described may be purely superficial and illusory. Secondly, the two diseases may have been superposed in the case of the striped plants from which the organism was obtained, the method of cultivation adopted by the authors having destroyed the virulence of the parasite so that infection was not obtained. Thirdly, the two organisms are actually identical, the organism being really a saprophyte and growing so strongly in the dead tissue and in artificial culture as to mask the presence of the true parasite. The authors put forward the third suggestion with great hesitation in view of the wide experience of Dr Smith and of the obvious care exhibited in all his work. In this case, however, many of his recorded inoculations seem to have been made by an assistant, and with material derived by crushing diseased tissue. Again, the very viscid nature of the growth of the organism in artificial culture would tend to make one suspicious of the purity of colonies appearing on a plate since such a slime might well conceal a second organism, especially such a one as *Bacillus lathyri*, whose size and shape are so closely similar to those of *Aplanobacter michiganense*. The authors are emboldened to put forward this view by the statement of Smith that "when this organism was first discovered the writer thought he observed motility."

Supposing that *Aplanobacter michiganense* were proved to be a saprophyte the question would arise as to the possible identity of "Stripe Disease" with the "Grand Rapids Disease." On the face of it such a possibility seems to be a remote one. In Smith's account of his disease no mention is made of any external markings either on the stem or the fruit. These are such a very distinct feature of "Stripe" that they could not possibly have been overlooked. The morbid anatomy in the two cases is however identical; the photograph which appears in Smith's work(8), Fig. 72, p. 163, might well have been taken from a section of a "striped" plant. The lesions in the pith and the presence of bacteria which appear in the outer layers of the cortex are quite characteristic of "Stripe" disease.

Moreover, artificial inoculations of plants with *Bacillus lathyri* made in October, when the plants were well developed, have resulted in no more sign of disease than such lesions in the pith as are shown in this photograph. It is only when plants are growing rapidly that the typical stripes are produced upon the stems.

In view of the present work therefore it seems highly desirable that a further investigation of the Grand Rapids Disease should be carried out.

SUMMARY.

(1) A Stripe disease of tomatoes growing under glass is described.

(2) The causal organism is a small yellow bacillus believed to be identical with *Bacillus lathyri*, Manns and Taubenhaus.

(3) The effect of manurial treatment on the incidence of the disease shows that excess of nitrogen increases susceptibility in the plant and this can be largely counteracted by increase of potash.

(4) Different varieties of tomatoes show varying degrees of susceptibility to the disease.

(5) It is tentatively suggested that the Grand Rapids Tomato Disease, described by Smith, may be identical with this Stripe disease and that the organism which has been described as the cause of the Grand Rapids Disease may prove to be a saprophyte.

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NOTES ON THE LIFE-HISTORY OF *EPHESTIA KUHNIELLA.*

By RAYMOND V. WADSWORTH.

Very little has been recorded of the life-history of this moth, although it is so well known and of such economic importance. The writer having had for some years experience of the moth as a warehouse pest, and in breeding experiments, thought that the following record would be of value.

The moth flies during any time of the day or night. Its flight seems to be particularly aimless, as it is not drawn to any of the common devices used to attract insects. Although it has been stated in the *Gordian* that it is attracted by light, the writer has not been able to obtain the least success by this method, and it seems likely that some other small moth was mistaken for *E. kuhniella*. During its life the moth needs no food of any kind, and very seldom if ever takes any, which probably explains the failure of many of the methods of insect capture. It is slow and heavy in its flight, though it can sustain its flight for a considerable time. Above all things, it loves a very still atmosphere. In secluded corners and small recesses where the air is hardly moving, and the atmosphere heavy, the moth abounds and enjoys it to the full, whilst in draughty places scarcely one can be found. Generally it finds its way out of the open into some secluded spot. Cupboards and boxes provide a paradise for it. This dislike of moving air has been hinted at by J. H. Durrant, of the British Museum, in his report on the Army Biscuit question, but not sufficiently emphasised.

The moth lives about a month, laying its eggs towards the latter half of its existence. The eggs are white, 0·0197 in. by 0·0145 in., easily visible to the naked eye, and under the microscope very prettily wrinkled. In laying the eggs the moth does not necessarily display any great maternal feeling, for it will often lay them at a considerable distance from food. Generally however they are placed on the food stuff, singly and not in groups. When the food is in sacks, there are generally holes

through which the moth can lay its eggs, but failing this it will lay them on the sacking. The eggs are laid in the darkest corners, as far from the light as possible, and where the material chosen provides cracks and crevices they are placed in these. Thus they are well protected from crushing and from being seen. Never does the moth lay its eggs exposed to the strong light of day.

The larva hatches in a week or so, according to the temperature. If already on food it commences feeding almost at once. If however it is not, or if the food on which it hatches is too hard for its young jaws, it wanders off in search of something sufficiently tender for its delicate age. The outside shell of a cocoa bean, for instance, is too hard for the newly-hatched larva, which will search for a broken shell if born on a bean whose testa is perfect.

Having found its food, the larva with no further ado commences to feed, and eating straight ahead bores its way into the food, leaving only a small hole as evidence of its presence. After a few days it spins itself a silken tube, in which it lives and from which it feeds, and which, if food in its immediate neighbourhood is plentiful, it seldom leaves before it is full-fed. In flour, and such-like fine material, these silk tubes are generally pretty near the surface, but with beans and similar material the tubes are inside the bean, and well inside the bag. At this period of its history, the effect of the larva is not at all evident. The larva is very stationary in its habits, and so the food, especially if it be in bags, appears hardly touched. No larvae are seen, and the silken webbing, so characteristic, is not present. This webbing, so noticeable in most warehouses, is made practically wholly by the full-fed larva in search of a place in which to pupate. The larva loves still air, like the moth, and above all things, darkness. If exposed to the light, it will stop feeding and search for a dark place.

The food of the larva presents interesting variations and influences, as much as the temperature, its length of life. Known as the "Mediterranean Flour Moth," one is apt to think of it as only a flour pest, whereas, as a matter of fact, it is much more widely distributed. It will attack all starchy foods, such as grains of all kinds, dried vegetables, cocoa beans and nuts, and will also feed on jelly cubes and chocolate. The writer has found no instance of its attacking any animal food stored in warehouses, but one peculiarity of its diet suggests that this might be possible. Whenever the larva comes in contact with a dead moth, it accepts the discovery as a delicacy in its diet, no matter what other food is at hand,

and proceeds to make a meal of it. In one instance, the writer kept larvae fed only on Ephestia and Tortrix, for some six weeks. They accepted the diet and outgrew other larvae hatched at the same time and fed on dried beetroot—a favourite food. It thus seems that the larva is fairly broad in its food list, and is unfortunately no epicure. This of course increases the seriousness of the pest, and makes its extermination more difficult. The larva will change its diet fairly readily; from a hard food to a soft food it will change with ease and rapidly settle down, but *vice versa*, though ultimately it will become accustomed to its new food, it will wander far in search of something more to its liking.

The length of life of the larva is generally accepted as being about ten to twelve weeks, but very varying lengths have been given by different authorities. Sharp gives ten weeks or even less, whilst Durrant gives as long as eighteen weeks. The difference arises from the effect of food and temperature. Sharp says, "The enormous increase being due in all probability to the fact that the favourable conditions and equable temperature in the mills promote a rapid succession of generations." It would be well to add favourable food to the above conditions. Under these circumstances there can be as many as six generations in the year, but under more natural conditions the number of generations can be reduced to one per annum. Even however given constant conditions of food and temperature, some larvae will grow very much more quickly than others. Often, larvae will in six weeks reach twice the size of others hatched at the same time. This happens more obviously under poor conditions than under good ones, and of course means the necessary overlapping of generations. The writer has found that very hard foods, such as dried potatoes, will abnormally prolong the life cycle, so that not even one generation is produced in a year. In ordinary circumstances dried potatoes are practically never attacked, even though presenting ideal conditions.

When the larva is full fed, it leaves its silken case and the food on which it has been feeding and goes in search of a safe place in which to pupate. Very seldom indeed does it pupate where it feeds. It is at this stage that the presence of the larva is very noticeable. The bags and walls become covered with silken threads, and numbers of fat and well-grown larvae are to be seen wandering over floors and walls and bags. This exodus in a cool store takes place in August and September, but in hot stores takes place more or less all the time. After some days'

wandering the larva has found its place and spins its cocoon inside which it lies with its ventral surface uppermost. Perhaps the favourite spot for *E. kuhniella* is the ears of sacks, where the cocoons can be found crowded together in great numbers, looking almost like one large cocoon; but any suitable crevice will do. If it is autumn, the larva may remain as it is inside the cocoon until next spring, or it may pupate and hatch out almost at once, taking about a fortnight to do so. In the latter case, the insect pairs and lays its eggs at once. These generally hatch, and the winter is passed in the larval form

NOTES.

By J. C. F. FRYER.

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1. *Charaeas graminis*, L.

Statements as to the stage in which this well-known pest passes the winter are conflicting. Most continental writers suggest that the eggs hatch within a month of the time they are laid (August –September) and that the species hibernates as a young larva. English entomologists, on the other hand, with the exception of Miss Ormerod, state that hibernation takes place in the egg stage. Under the circumstances the following observations may be of interest. A female *C. graminis* captured at Richmond (Surrey) in September, 1918, laid about sixty eggs which were divided into two batches. One batch was placed on a small piece of flower-pot and except for the protection afforded by a cover of perforated zinc was fully exposed to the weather. The other batch was kept in a dry, unheated shed in a glass jar. The latter batch received no moisture while the former was constantly soaked by rain. Although the conditions were different in the case of the two batches, hatching began on the same day—April 7th, 1919, and the great majority of the larvae left the egg within the two succeeding days. No larvae were hatched in the autumn. It would therefore seem that *C. graminis* passes the winter in the egg stage, a point which has a definite economic bearing. Imms and Cole (*Journ. Board of Agriculture*, XXIV, No. 5) suggest that the recent outbreaks of Antler Moth in Derbyshire and other districts are to a considerable extent due to the cessation during the war of the custom of burning hill pastures during March and April. The fact that the eggs of *C. graminis* hatch in April supports this view, for while hibernating larvae buried in tufts of grass or hidden under stones might probably escape the effects of a superficial burning, the eggs or newly hatched larvae would be much more likely to succumb.

2. *Sitotroga cerealella*, Oliv.

This small moth, often known as the "Angoumois Grain Moth," is regularly imported into Great Britain by means of infested cargoes of

grain—notably of maize—from America where it has proved a serious pest. In the warmer countries of the world it breeds in the open, in the grain fields, but in temperate regions its increase is confined to warehouses, etc., in which the temperature remains fairly high. It was therefore a surprise when, in October, 1918, two specimens of the moth emerged from some ears of barley grown on a small experimental plot near Kew. The pupae from which the moths had emerged were discovered in the ears and from the circumstances under which the latter were obtained there is no doubt but that the eggs must have been laid on the standing crop in the field. The probable explanation is that moths had emerged from infested grain on one of the barges passing up the Thames and by chance had discovered the barley. There is little likelihood of the species becoming a field pest in the British Isles but its breeding in the open is perhaps worth putting on record.

3. *Anthonomus pomorum*, L.

There seems to be a need for further observations on the habits of the adult beetles of this species during the time which elapses between their emergence from the pupae and their entry into hibernation. Among other points the extent to which the insects feed seems to have been disputed and it may therefore be of interest to record that in captivity a number of the weevils fed actively on apple foliage, attacking the undersides of the leaves but leaving the upper cuticle and the veins. On the other hand beetles kept without food all died. While dealing with *Anthonomus* it may also be worth recording that the beetles on which the above notes were made were obtained as larvae and pupae from an orchard in Hereford which was very seriously attacked. No accurate attempt was made to record the percentage of weevils killed by the parasite *Pimpla pomorum* Ratz., but it was certainly less than 1 per cent. in marked contrast to figures obtained from a Cambridgeshire sample recorded by Imms in a previous number of this Journal (vol. IV, p. 211).

4. *Phyllobius urticae*, De G., and *P. oblongus*, L.

For several years about thirty acres of strawberries on a large fruit plantation in Hereford have suffered very seriously from the attacks of weevil larvae at the roots, the damage in one year being estimated at £1000. Examples of the larvae were examined in March, 1919, and although they exhibited minor differences which appeared to separate them from *Otiorrhynchus sulcatus*, F. and *O. picipes*, F. they were nevertheless attributed to that genus. On May 15th, however, adults began to appear in the breeding cages and in all cases proved to be

members of the genus *Phyllobius*, *P. urticae* being the predominant species with a few *P. oblongus* in addition. About the same date the owner of the plantation wrote to say that he also had been breeding out adult winged weevils but in his case all appeared to be *P. oblongus*. Unfortunately no examination of the plantation was made until June 6th, when *P. oblongus* was still present in large numbers but *P. urticae* appeared to have gone, none being found even in the adjacent hedgerows. The plantation had been sprayed very heavily with lead arsenate and it was said that vast numbers of *P. oblongus* had been killed.

At this time curiously enough there were still a few larvae indistinguishable from those of *Phyllobius* at the roots of the strawberries, but none have been reared and their identity is therefore unknown.

Larvae of the genus *Phyllobius* do not in the past seem to have been regarded as of much economic importance either in Britain or on the continent. Reh (in Sorauer's *Handbuch der Pflanzekrankheiten*, III, p. 544) says that they are not harmful with the exception of those of *P. glaucus*, Scop. (*P. calcaratus*, F.) which he records on the authority of Ritzema Bos as having caused damage to the roots of strawberries. However, this note is written without any extensive reference to the literature on the genus and it is possible that there is more information available.

REVIEW.

Miyake, T. "Studies on the Fruit-flies of Japan. I. Japanese Orange Fly." *Bull. Imp. Agric. Sta. Japan*, Vol. II, 1919, pp. 85–165, Plates II–X.

This excellent and well illustrated monograph deals with the Japanese fruit-fly, *Dacus tsueonis* sp. nov. The insect is described in detail, and the author also gives a good description of the external structure and an account of the alimentary and reproductive systems. The larva is discussed very fully and a good deal of information is given of its internal and external anatomy. In the bionomics of the fly some interesting features are brought to light. Thus, the imagines are strongly attracted to citronella oil, like those of several other species of the genus. Raspberry syrup is apparently almost equally attractive, but kerosene has little or no value in this respect.

There appears to be but a single generation in the year, and the species is limited to the island of Kiusiu in its distribution. Its destructiveness usually amounts to from 10 % to 20 % of the orange crop, but when severe it reaches 50 %. The ovipositor pierces the skin of the fruit and reaches the pulp, where the eggs are laid; thick-skinned oranges are for this reason usually exempt from attack. When the larva is fully grown, the infested fruit falls, and pupation takes place in the soil. No certain parasites of this insect have so far been discovered. The author recommends capturing the flies by means of a kind of racquet smeared with bird-lime; infested fruits should be collected as soon as possible, and can be utilised for the preparation of citric acid. Storehouses should be improved and provided with hard floors, in order to prevent any larvae issuing from infested fruit from entering the earth for purposes of pupation. The paper concludes with descriptions of five new Japanese Trypaneidae.

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